ISSN 1346-7565

Acta Phytotax. Geobot. 68 (3): 145–174 (2017)
doi:10.18942/apg.201706

Systematic Study of the *Yakushimabryum* and Related Genera in the Pylaisiadelphaceae (Bryophyta)

Hiroyuki Akiyama

*Museum of Nature and Human Activities, Hyogo / Institute of Environmental Sciences, University of Hyogo, Yayoigaoka-6, Sanda, Hyogo 669-1546, Japan. *akiyama@hitohaku.jp*

Phylogenetic relationships among the members of the epiphytic genus *Yakushimabryum* H. Akiyama *et al.* and related genera (Pylaisiadelphaceae) were studied using cpDNA (*rbcL*, *rps4*, and *trnL-F*) gene sequences as well as morphological features. Present analyses (1) suggested the presence of three clades in the Pylaisiadelphaceae and Sematophyllaceae (Pylaisiadelphaceae *s. str.*, Sematophyllaceae *s. str.* + Heterophyllioideae, and *Clastobryum*), and (2) confirmed the distinctive generic status of *Yakushimabryum* from other members of the family. One new genus *Orientobryum* H. Akiyama and two new species *O. ovalifolium* H. Akiyama and *Y. brevigemmium* H. Akiyama were recognized and described. In addition, a close inter-relationship of *Pseudotrismegistia undulata* (Broth. & Yasuda) H. Akiyama & Tsubota and *Heterophyllium amblystegum* (Mitt.) J. Yu *et al.* (= *Mastopoma subfiliferum* Horik. & Ando) was confirmed. Four new combinations, *O. oligonema* (Cardot & P. de la Varde) H. Akiyama (≡ *Clastobryum oligonema* Cardot & P. de la Varde), *Y. subintegrum* (P. Tixier) H. Akiyama (≡ *Aptychella subintegra* P. Tixier), *Y. tonkinense* (Broth.) H. Akiyama (≡ *Clastobryum tonkinense* Broth. & Paris), and *Pseudotrismegistia amblystega* (Mitt.) H. Akiyama (≡ *Stereodon amblystegus* Mitt.) were proposed.

Key words: *Clastobryum, Gammiella*, Heterophyllioideae, *Orientobryum oligonema*, *Orientobryum ovalifolia*, *Pseudotrismegistia amblystega*, *Yakushimabryum brevigemmium*, *Yakushimabryum subintegrum*, *Yakushimabryum tonkinense*

Recent progress in molecular phylogeny has shown its strength in revealing relationships and has given new insights into pleurocarpous bryophyte systematics (Tsubota *et al.* 2000, 2001a, b, 2002, Shaw *et al.* 2003, Ignatov *et al.* 2007, O'Brien 2007, Olsson *et al.* 2009, Merget & Wolf 2010, Ho *et al.* 2012, Huttunen *et al.* 2013, and many others). As for the Hypnales, which includes most species of pleurocarpous mosses, however, persuasive outcomes have been less successful because of little genetic differentiation among species, genera, and even families.

The Pylaisiadelphaceae are one of the members of the Hypnales. The family was first established by Goffinet & Buck (2004), distinguishing it from its close relative, Sematophyllaceae, by scarcely inflated, smaller alar cells often arranged in a scalariform manner (except for *Clastobryum*), the frequent presence of filamentous pseudoparaphyllia, and by non-collenchymatous exothecial cells. Most of the members are epiphytic and form small populations geographically distantly separated from each other. It is one of the reasons why the family includes a number of endangered species, for example, *Aptychella robusta* (Broth.) M. Fleisch., *Clastobryum glabrescens* (Z. Iwats.) B. C. Tan, Z. Iwats. & D. H. Norris, and *Gammiella ceylonensis* (Broth.) B. C. Tan & W. R. Buck, in Japan (Ministry of the Environment 2015). Previous phylogenetic analyses based on molecular markers (*rps4* and *nad5*) suggested the non-monophyletic nature of the Pylaisiadelphaceae (Cox *et al*. 2000). On the other hand, several genera of the family, such as *Aptychella* (Broth.) Herzog (Akiyama *et al*. 2015) and *Taxithelium* Spruce ex Mitt. (Câmara 2011), have been subjected to detailed molecular phylogenetic analyses.

The main objectives of this paper are (1) to examine the relationships among the members previously classified in the Pylaisiadelphaceae and Sematophyllaceae, and (2) to reveal the taxonomic positions of *Yakushimabryum longissimum* H. Akiyama, Y. Chang, T. Yamag. & B.C. Tan (Akiyama 2014, Akiyama *et al*. 2011) and *Gammiella tonkinensis* (Broth.) B. C. Tan & W. R. Buck (Tan & Buck 1989), along with a pendulous morph of the latter species formerly recognized as *G. touwii* B. C. Tan (Tan 1990) in a broader perspective. *Yakushimabryum* was first established by Akiyama *et al*. (2011). Suzuki *et al*. (2013) synonymized *Y. longissimum*, the sole species of the genus, under *Gammiella tonkinensis*. Akiyama (2014) and Akiyama *et al*. (2015) disagreed with that conclusion and provided additional evidence from external morphology and molecular phylogenic data to support the recognition of *Yakushimabryum* as a genus separate from *Gammiella* and *Aptychella*. Therefore, a larger scale analysis with extensive taxon sampling, mainly from the Pylaisiadelphaceae and Sematophyllaceae, was planned. In addition, I have recognized that some specimens of *Clastobryum* species were misidentified as *Gammiella tonkinensis* in the course of examination of a number of herbarium specimens. This is the reason for including *Clastobryum oligonema* in the analysis.

Materials and Methods

Examination of herbarium specimens

A number of herbarium specimens, including types, which were used to fix nomenclatural issues, were borrowed from the following herbaria; BM, FH, H, HIRO, HYO, KYO, L, NICH, NY, PC, SING, SINU, and TNS.

Taxon sampling for molecular analyses

Most of the examined samples for DNA sequence analyses were extracted directly from plants newly collected by me or in a few cases from recently (less than five years) collected herbarium specimens. Field studies, with permission to make collections, were carried out at Doi Inthanon National Park in northern Thailand, Bidoup-Nui Ba National Park in southern Vietnam, Tam Dao National Park in northern Vietnam, the Cameron Highlands, Genting Highlands, and Mt. Kinabalu in Malaysia, Dongyan Shan in northern Taiwan, Syuejin and Dasyue Shan in central Taiwan, as well as several localities in southwestern Japan.

The phylogenetic analyses were aimed at determining the taxonomic positions of *Yakushimabryum longissimum* and *Gammiella tonkinensis* and their relationship to each other and to previously described species, such as *Gammiella touwii* B. C. Tan and *Aptychella subintegrum* P. Tixier. Therefore, 14 populations of *Y. longissimum s. lat*. (including two of *G. touwii* and two of *A. subintegra*) and 19 of *Gammiella tonkinensis* were included in the present study (Appendix). In addition, a single specimen collected in northern Vietnam (as *Y. brevigemmium* in Figs. 1 & 2) was also included. Five species from *Aptychella* were also included based on the results of Akiyama *et al.* (2015). Seven samples of *Clastobryum oligonema* Cardot & P. de la Varde, which has been often confused with *G. tonkinensis* and synonymized under *Aptychella tenuiramea* (Mitt) Tixier based on insufficient evidence (Tixier 1977), were also included in the analyses to determine the actual relationship to *G. tonkinensis*.

As in the case of Akiyama *et al*. (2015), I selected ingroup terminals from the members of the Sematophyllaceae in a broad sense, that is, Sematophyllaceae *s. str*. and Pylaisiadelphaceae (Goffinet *et al.* 2009). In addition, I included three species of *Clastobryum* Dozy & Molk., i.e., *C. scalare* (Müll. Hal.) Tixier (two samples), *C. glabrescens* (Z. Iwats.) B. C. Tan, Z. Iwats. & D. H. Norris, and *C. spiculiferum* (Dixon) B. C. Tan, Z. Iwats. & D. H. Norris in the present analyses.

They were included to better understand the relationship of *Clastobryum oligonema* to *Gammiella tonkinensis*; the latter was once recognized as a member of *Clastobryum*. In addition, *Fauriella tenuis* (Mitt.) Cardot was included since Li *et al.* (2014) revealed its affinity to the Pylaisiadelphaceae. As a result, I included a total of 20 genera that have been recognized as members of the Pylaisiadelphaceae and Sematophyllaceae. As for the Pylaisiadelphaceae, 12 out of 15 genera previously recognized in the family (Goffinet *et al.* 2009) were included in the present analyses. *Climacium dendroides* (Hedw.) F. Weber & D. Mohr (Climaciaceae) and *Pleuroziopsis ruthenica* (Weinm.) Kindb. ex E. Britton (Pleuroziopsiaceae) were used as outgroup terminals (Cox *et al.* 2000). A total of 83 samples (22 genera and 43 species) were used in the present analysis. Voucher information for the newly registered accessions in DDBJ are provided in the Appendix.

DNA extraction, amplification, and sequencing

DNA extraction and amplification followed the same methods described in Akiyama *et al.* (2015). Nucleotide sequences were newly obtained from 64 samples for this study, including 192 nucleotide sequences (Appendix). Sequenced regions are: (1) the plastid *trnS-rps4* region [i.e., *rps4* plus the *trnS-rps4* intergenic spacer (IGS), hereafter *rps4*], (2), the plastid *trnL-F* region, including the trnLUAA group I intron and the *trnL-F* IGS (hereafter *trnL-F*), and (3) the ribulose bisphosphate carboxylase large chain (hereafter *rbcL*).

I used MUSCLE (Edgar 2004) to manually align the final consensus sequences, together with previously published sequences obtained from NCBI via an internet web browser implemented in MEGA 7.0.21 (Kumar *et al.* 2016). After alignment, completely identical sequences were removed to reduce node-density artifact in the phylogenetic analyses (Fitch & Beintema 1990).

Phylogenetic analyses

Preliminary analyses using *rps4* (DNA substitution model T92+G; Tamura 1992), *trnL-F* (T92+G+I), and *rbcL* (T93N+G+I; Tamura & Nei 1993) datasets separately yielded no conflicting branches with high bootstrap support or posterior probabilities and thus combined data sets of all three sequences were used for further analyses. There was no ambiguity in the alignment except for hyper variable sites of *trnL-F*, which were deleted and not used in the analyses. Gaps in the alignment were treated as missing data.

I performed Maximum Likelihood (ML) and Maximum Parsimony (MP) analyses using MEGA 7.0.21 (Kumar *et al.* 2016) with the option of partial deletion (PD; site coverage cutoff 95%) for missing data, and Baysian (BI) analyses using MrBayes ver. 3.2.2 (Ronquist & Huelsenbeck 2003). For MP analyses, I used default settings with TBR branch-swapping with 1,000 random addition replicates. I used T92+G+I model in the ML analysis, which were determined as the optimal model according to the Akaike's Information Criterion (AIC: Akaike 1973) as implemented in MEGA 7.0.21. I did non-parametric bootstrapping analyses for ML and MP analyses. This was performed with 200 pseudo-replicates with simple taxon additions in both ML and MP analyses. For BI analysis, I used T92+G+I model with 10,000,000 generations; trees were sampled every 1,000 generations. The first 12,500 trees were removed for the burn-in phase. Bayesian posterior probability was calculated as node support values.

Results

The sequences obtained ranged from 600–689 bps for *rps4* (83 samples), 421–454 bps for *trnL-F* (81 samples), and 1,278–1,350 bps for *rbcL* (82 samples). The aligned combined matrix of the three loci along with sequences from the NCBI database comprised 2,316 bps: 625 bps for *rps4*, 413 bps for *trnL-F*, and 1,278 bps for *rbcL*. Of them, 55 had unique information, and 28 were redundant. The unique 55 sequences were actually used for the phylogenetic inference.

As a result, the single most parsimonious tree

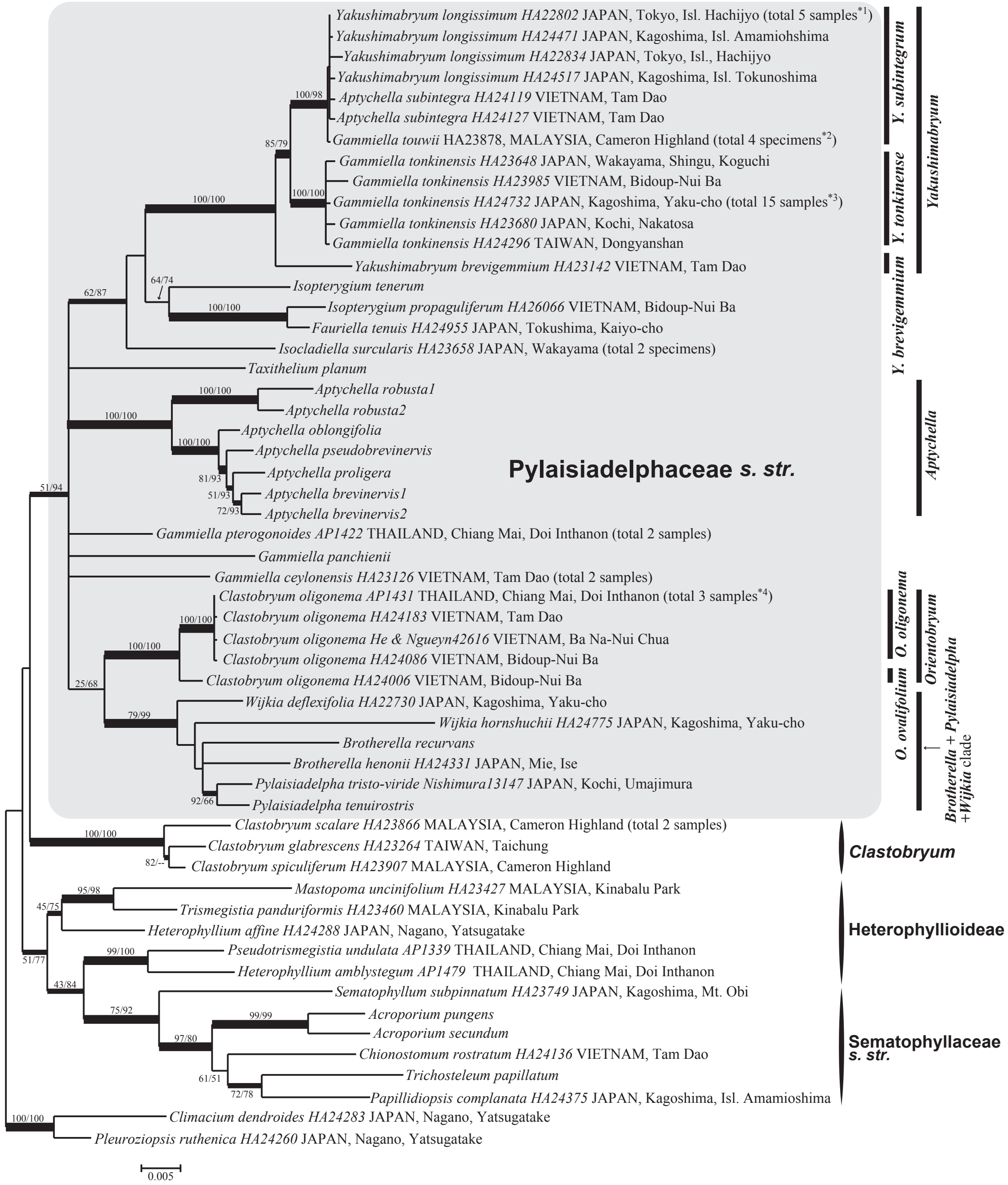
Yakushimabryum longissimum HA22802 JAPAN, Tokyo, Isl. Hachijyo (total 5 samples*1)
Yakushimabryum longissimum HA24471 JAPAN, Kagoshima, Isl. Amamiohshima
Yakushimabryum longissimum HA22834 JAPAN, Tokyo, Isl., Hachijyo
Yakushimabryum longissimum HA24517 JAPAN, Kagoshima, Isl. Tokunoshima
Aptychella subintegra HA24119 VIETNAM, Tam Dao
Aptychella subintegra HA24127 VIETNAM, Tam Dao
Gammiella touwii HA23878, MALAYSIA, Cameron Highland (total 4 specimens*2)
Gammiella tonkinensis HA23648 JAPAN, Wakayama, Shingu, Koguchi
Gammiella tonkinensis HA23985 VIETNAM, Bidoup-Nui Ba
Gammiella tonkinensis HA24732 JAPAN, Kagoshima, Yaku-cho (total 15 samples*3)
Gammiella tonkinensis HA23680 JAPAN, Kochi, Nakatosa
Gammiella tonkinensis HA24296 TAIWAN, Dongyanshan
Yakushimabryum brevigemmium HA23142 VIETNAM, Tam Dao
Isopterygium tenerum
Isopterygium propaguliferum HA26066 VIETNAM, Bidoup-Nui Ba
Fauriella tenuis HA24955 JAPAN, Tokushima, Kaiyo-cho
Isocladiella surcularis HA23658 JAPAN, Wakayama (total 2 specimens)
Taxithelium planum
Aptychella robusta1
Aptychella robusta2
Aptychella oblongifolia
Aptychella pseudobrevinervis
Aptychella proligera
Aptychella brevinervis1
Aptychella brevinervis2
Gammiella pterogonoides AP1422 THAILAND, Chiang Mai, Doi Inthanon (total 2 samples)
Gammiella panchienii
Gammiella ceylonensis HA23126 VIETNAM, Tam Dao (total 2 samples)
Clastobryum oligonema AP1431 THAILAND, Chiang Mai, Doi Inthanon (total 3 samples*4)
Clastobryum oligonema HA24183 VIETNAM, Tam Dao
Clastobryum oligonema He & Ngueyn42616 VIETNAM, Ba Na-Nui Chua
Clastobryum oligonema HA24086 VIETNAM, Bidoup-Nui Ba
Clastobryum oligonema HA24006 VIETNAM, Bidoup-Nui Ba
Wijkia deflexifolia HA22730 JAPAN, Kagoshima, Yaku-cho
Wijkia hornshuchii HA24775 JAPAN, Kagoshima, Yaku-cho
Brotherella recurvans
Brotherella henonii HA24331 JAPAN, Mie, Ise
Pylaisiadelpha tristo-viride Nishimura13147 JAPAN, Kochi, Umajimura
Pylaisiadelpha tenuirostris
Clastobryum scalare HA23866 MALAYSIA, Cameron Highland (total 2 samples)
Clastobryum glabrescens HA23264 TAIWAN, Taichung
Clastobryum spiculiferum HA23907 MALAYSIA, Cameron Highland
Mastopoma uncinifolium HA23427 MALAYSIA, Kinabalu Park
Trismegistia panduriformis HA23460 MALAYSIA, Kinabalu Park
Heterophyllium affine HA24288 JAPAN, Nagano, Yatsugatake
Pseudotrismegistia undulata AP1339 THAILAND, Chiang Mai, Doi Inthanon
Heterophyllium amblystegum AP1479 THAILAND, Chiang Mai, Doi Inthanon
Sematophyllum subpinnatum HA23749 JAPAN, Kagoshima, Mt. Obi
Acroporium pungens
Acroporium secundum
Chionostomum rostratum HA24136 VIETNAM, Tam Dao
Trichosteleum papillatum
Papillidiopsis complanata HA24375 JAPAN, Kagoshima, Isl. Amamioshima
Climacium dendroides HA24283 JAPAN, Nagano, Yatsugatake
Pleuroziopsis ruthenica HA24260 JAPAN, Nagano, Yatsugatake
100/98
85/79
100/100
100/100
62/87
64/74
100/100
100/100
100/100
100/100
81/93
51/93
72/93
51/94
100/100
100/100
25/68
79/99
92/66
100/100
82/--
95/98
45/75
51/77
99/100
43/84
75/92
99/99
97/80
61/51
72/78
100/100
0.005
Pylaisiadelphaceae s. str.
Y. subintegrum
Yakushimabryum
Y. tonkinense
Y. brevigemmium
Aptychella
O. oligonema
Orientobryum
O. ovalifolium
Brotherella + Pylaisiadelpha +Wijkia clade
Clastobryum
Heterophyllioideae
Sematophyllaceae s. str.

FIG. 1. Phylogeny of 55 selected taxa inferred by *rps4*, *trnL-F*, and *rbcL* sequences based on ML analysis. BSML and BSMP are shown. Branches with both BSML and BSMP ≥ 70 are indicated by thickest lines, those with either BSML or BSMP ≥ 70 by medium lines. *1 = *Yakushimabryum subintegrum* voucher 1, 2 and 4–6. *2 = *ditto*. 7–10. *3 = *Y. tonkinense* voucher 1–8, 10–12 and 14–17. *4 = *Orientobryum oligonema* voucher 2, 3 and 5.

from the MP analysis was 990 steps in length (CI= 0.451220, RI = 0.759744). Trees from the ML and MP analyses, with high support values, did not differ in topology, thus the tree inferred from the ML analysis was used to represent both results (Fig. 1). A tree from the BI analysis dif-

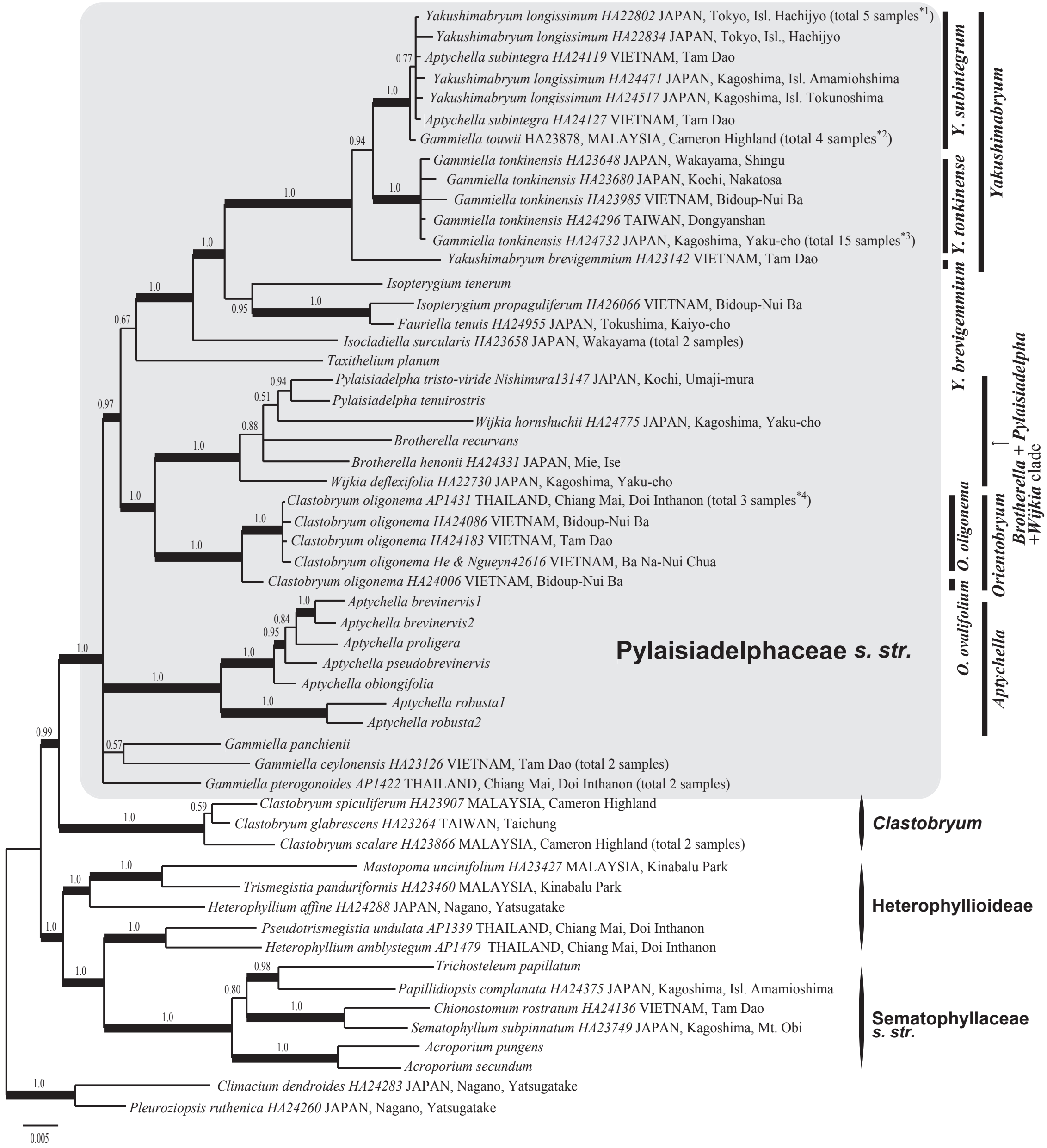
Yakushimabryum longissimum HA22802 JAPAN, Tokyo, Isl. Hachijyo (total 5 samples*1)
Yakushimabryum longissimum HA22834 JAPAN, Tokyo, Isl., Hachijyo
0.77
Aptychella subintegra HA24119 VIETNAM, Tam Dao
Yakushimabryum longissimum HA24471 JAPAN, Kagoshima, Isl. Amamiohshima
1.0
Yakushimabryum longissimum HA24517 JAPAN, Kagoshima, Isl. Tokunoshima
Aptychella subintegra HA24127 VIETNAM, Tam Dao
0.94
Gammiella touwii HA23878, MALAYSIA, Cameron Highland (total 4 samples*2)
Gammiella tonkinensis HA23648 JAPAN, Wakayama, Shingu
Gammiella tonkinensis HA23680 JAPAN, Kochi, Nakatosa
1.0
1.0
Gammiella tonkinensis HA23985 VIETNAM, Bidoup-Nui Ba
Gammiella tonkinensis HA24296 TAIWAN, Dongyanshan
1.0
Gammiella tonkinensis HA24732 JAPAN, Kagoshima, Yaku-cho (total 15 samples*3)
Yakushimabryum brevigemmium HA23142 VIETNAM, Tam Dao
1.0
Isopterygium tenerum
0.67
0.95
1.0
Isopterygium propaguliferum HA26066 VIETNAM, Bidoup-Nui Ba
Fauriella tenuis HA24955 JAPAN, Tokushima, Kaiyo-cho
Isocladiella surcularis HA23658 JAPAN, Wakayama (total 2 samples)
Taxithelium planum
0.94
Pylaisiadelpha tristo-viride Nishimura13147 JAPAN, Kochi, Umaji-mura
0.97
0.51
Pylaisiadelpha tenuirostris
0.88
Wijkia hornshuchii HA24775 JAPAN, Kagoshima, Yaku-cho
1.0
Brotherella recurvans
Brotherella henonii HA24331 JAPAN, Mie, Ise
1.0
Wijkia deflexifolia HA22730 JAPAN, Kagoshima, Yaku-cho
Clastobryum oligonema AP1431 THAILAND, Chiang Mai, Doi Inthanon (total 3 samples*4)
1.0
Clastobryum oligonema HA24086 VIETNAM, Bidoup-Nui Ba
1.0
Clastobryum oligonema HA24183 VIETNAM, Tam Dao
Clastobryum oligonema He & Ngueyn42616 VIETNAM, Ba Na-Nui Chua
Clastobryum oligonema HA24006 VIETNAM, Bidoup-Nui Ba
1.0
Aptychella brevinervis1
0.84
Aptychella brevinervis2
0.95
Aptychella proligera
1.0
1.0
Aptychella pseudobrevinervis
Pylaisiadelphaceae s. str.
1.0
Aptychella oblongifolia
1.0
Aptychella robusta1
Aptychella robusta2
0.99
0.57
Gammiella panchienii
Gammiella ceylonensis HA23126 VIETNAM, Tam Dao (total 2 samples)
Gammiella pterogonoides AP1422 THAILAND, Chiang Mai, Doi Inthanon (total 2 samples)
0.59
Clastobryum spiculiferum HA23907 MALAYSIA, Cameron Highland
1.0
Clastobryum glabrescens HA23264 TAIWAN, Taichung
Clastobryum
Clastobryum scalare HA23866 MALAYSIA, Cameron Highland (total 2 samples)
1.0
Mastopoma uncinifolium HA23427 MALAYSIA, Kinabalu Park
1.0
Trismegistia panduriformis HA23460 MALAYSIA, Kinabalu Park
Heterophyllium affine HA24288 JAPAN, Nagano, Yatsugatake
Heterophyllioideae
1.0
1.0
Pseudotrismegistia undulata AP1339 THAILAND, Chiang Mai, Doi Inthanon
Heterophyllium amblystegum AP1479 THAILAND, Chiang Mai, Doi Inthanon
1.0
0.98
Trichosteleum papillatum
0.80
Papillidiopsis complanata HA24375 JAPAN, Kagoshima, Isl. Amamioshima
1.0
Chionostomum rostratum HA24136 VIETNAM, Tam Dao
1.0
Sematophyllum subpinnatum HA23749 JAPAN, Kagoshima, Mt. Obi
Sematophyllaceae s. str.
1.0
Acroporium pungens
Acroporium secundum
1.0
Climacium dendroides HA24283 JAPAN, Nagano, Yatsugatake
Pleuroziopsis ruthenica HA24260 JAPAN, Nagano, Yatsugatake
0.005
Y. subintegrum
Y. tonkinense
Y. brevigemmium
Yakushimabryum
O. oligonema
O. ovalifolium
Orientobryum
Aptychella
Brotherella + Pylaisiadelpha +Wijkia clade

FIG. 2. Phylogeny of 55 selected taxa inferred by *rps4*, *trnL-F*, and *rbcL* sequences based on BI analysis. Branches with PPBI ≥ 0.95 are indicated by thick lines. *1 = *Yakushimabryum subintegrum* voucher 1, 2 and 4–6. *2 = *ditto.* 7–10. *3 = *Y. tonkinense* voucher 1–8, 10–12 and 14–17. *4 = *Orientobryum oligonema* voucher 2, 3 and 5.

fered from those from the ML and MP analyses and thus is shown separately (Fig. 2). Bootstrap values of ML (BSML) and MP (BSMP) analyses and posterior probabilities of BI analysis (PPBI) are shown on each node. In the following part, only clades supported by both ML/MP and BI analyses are mentioned.

Monophyly of Pylaisiadelphaceae and Sematophyllaceae

Members of the Pylaisiadelphaceae sensu Goffinet *et al.* (2009), such as *Aptychella*, *Brotherella*, *Clastobryum*, *Heterophyllium*, *Isocladiella*, *Isopterygium, Mastopoma*, *Pseudotrismegistia*, *Pylaisiadelpha*, *Taxithelium*, *Trismegistia*, and *Wijkia* as well as *Gammiella* and *Yakushimabryum* (Akiyama *et al.* 2011) and *Fauriella* (Li *et al.* 2014), did not form a monophyletic clade. Such groups except for three species of *Clastobryum* (*C. glabrescens*, *C. scalare*, and *C. spiculiferum*) as well as members of Heterophyllioideae (*Heterophyllium*, *Mastopoma*, *Pseudotrismegistia*, *Trismegistia*), however, formed weakly or highly supported monophyletic clades in the ML and MP analyses (BSML/BSMP = 51/94), respectively. BI analysis also suggested a highly supported monophyly both of the group (PPBI = 1.0) and the members of the Pylaisiadelphaceae including the above three species of *Clastobryum*, but excluding the members of the Heterophyllioideae (PPBI = 1.0).

On the other hand, although only six samples (five genera and six species) were used in the present analyses, the Sematophyllaceae *s. str.* formed a highly supported clade (BSML/BSMP = 75/92, and PPBI = 1.0).

Relationship of the Heterophyllioideae

Members of the subfamily Heterophyllioideae of the Pylaisiadelphaceae, such as *Heterophyllium affine*, *H. amblystegum*, *Pseudotrismegistia undulata*, and *Trismegistia panduriformis* as well as *Mastopoma uncinifolium* not only became paraphyletic but also were distantly related to the other members of the Pylaisiadelphaceae *s. str.* (Figs. 1 & 2).

Within the Heterophyllioideae, *Pseudotrismegistia undulata* and *Heterophyllium amblystegum* (= *Mastopoma subfiliferum*) formed a well supported clade (99/100, and 1.0). This clade became sister to the clade of Sematophyllaceae with poor to high support values (43/84, and 1.0). *Mastopoma uncinifolium* and *Trismegistia panduriformis* formed a well supported monophyletic clade (95/98, and 1.0). These two and *H. affine* formed a weak to highly supported clade (45/75, and 1.0) and this clade became sister to the above clade with weak to high support values (51/77, and 1.0).

It is notable that *Heterophyllium amblystegum* did not form a monophyletic clade with either *Mastopoma uncinifolium* or *H. affine*, but rather with *Pseudotrismegistia undulata* with high support values as already suggested by Akiyama & Tsubota (2001) based on *rbcL* sequence data.

Relationship between four species of Clastobryum

Four samples of three species of the genus *Clastobryum*, i.e., *C. glabrescens*, *C. spiculiferum* and *C. scalare*, became monophyletic with high support values (100/100, and 1.0). This clade was segregated from both the other members of Sematophyllaceae *s. str.* and Pylaisiadelphaceae *s. str.* In the BI analysis, this clade became sister to the clade of Pylaisiadelphaceae, excluding members of the Heterophyllioideae, with high support value (0.99). In the ML/MP analyses its relationship was not resolved. Its systematic position remains ambiguous because the present analyses did not include members of the other families of the Hypnales; more OTUs from the Hypnaceae and related families should be considered to determine its phylogenetic relationships in the Hypnales.

In contrast, seven samples of *Clastobryum oligonema* (Figs. 3–5 as *Orientobryum oligonema* and *O. ovalifolium*) collected in northern Thailand, southern, central, and northern Vietnam formed a well-supported clade (98/99/1.0). This clade was distantly related to the above three species of *Clastobryum.* In addition, judging from identifications of herbarium specimens, *C. oligonema* (Fig. 4i–j) was often confused with *Gammiella tonkinensis* (Fig. 7a–l). It is probably because they share similar leaf morphologies and filamentous gemmae with mammillose cells. They differ, however, in the length of the gemmae, as shown in Figs. 3 (g–h) and 7 (a–l). All the samples of *C. oligonema* and *G. tonkinensis* formed two separate clades and were not resolved as being closely related (Figs. 1 & 2). Within the clade of *Clastobryum oligonema*, one sample (*H. Akiyama 24006*) was segregated from the other with high support value (100/100, and 1.0). After examining the morphological features, it became evident that it had caducous branchlets as well as short filamentous gemmae, short acuminate ovate leaves, and weakly serrulate or mostly entire leaf margins, all of which differ from the ovate-lanceolate leaves with gradually narrowed apex and distinctly serrulate leaf margins in the other six samples. These six samples also lacked caducous branchlets.

Relationship among three genera Brotherella, Pylaisiadelpha, *and* Wijkia

Brotherella henonii, *B. recurvans* (= *Pylaisiadelpha recurvans*: Buck 1984), *P. tristo-viride*, two samples of *P. tenuirostris*, *Wijkia hornschuchii*, and *W. deflexifolia*, all of which share a *Brotherella*-type alar structure (with a single row of elliptic, more or less thin walled larger cells with 3 or 4 upper smaller and rectangular cells above), were revealed to form a monophyletic clade (BPW clade: Tsubota *et al*. 2001a) with high support values (79/99/, and 1.0). BI analysis suggested a close relationship of this group to the clade including seven samples of *Clastobryum oligonema* with high support values (PPBI = 1.0) but ML and MP analyses only weakly support the close relationship (25/68).

Relationship between five species of Gammiella

Five species of *Gammiella*, *G. pterogonioides*, *G. tonkinensis*, *G. touwii*, *G. panchienii* and *G. ceylonensis*, were analyzed and they did not form a monophyletic clade. Two samples of *G. pterogonioides* (type species of the genus) were not sister to the other four members. On the other hand, all 19 samples of *Gammiella tonkinensis* formed a well supported clade (100/100, and 1.0) sister to the clade including *Aptychella subintegra*, *G. touwii,* and *Yakushimabryum longissimum*.

Gammiella panchienii and *G. ceylonensis* remained ambiguous in the clade of Pylaisiadelphaceae *s. str.* in all three analyses.

Relationships within and between samples of Aptychella subintegra, Gammiella touwii, Yakushimabryum longissimum *and* Gammiella tonkinensis

Ten samples of *Yakushimabryum longissimum* (eight from southwestern Japan and two from Taiwan), two of *Gammiella touwii* (Peninsular Malaysia), and two of *Aptychella subintegra* (northern and southern Vietnam) formed a well-supported clade (100/98, and 1.0). All these three species share lanceolate leaves without distinct serration on the lower leaf margins and filamentous gemmae with rectangular smooth cells. Two samples of *Y. longissimum* collected in Taiwan (*H. Akiyama 23153-b* and *23284*) and the two of *G. touwii* collected in Malaysia (*H. Akiyama 23878* and *23913*) , however, formed a weakly supported subclade according to BI analysis (0.77). Two Taiwanese samples of *Y. longissimum* show slight differences in the shape of the gemmae and leaves: gemmae are smooth as in the other samples but shorter (Fig. 7m–r) and the lower leaf margins are weakly but distinctly serrulate.

As described above, a total of 19 samples of *Gammiella tonkinensis* (one from Taiwan, one from southern Vietnam and the others from central and southwestern Japan) also formed a well-supported clade (100/100/, and 1.0). The clade became sister to the above clade with moderate support values (85/79, 0.94).

One sample collected at Tam Dao National Park in northern Vietnam (*H. Akiyama 23142*, shown as *Yakushimabryum brevigemmium* in Figs. 1, 2 & 5), which looks morphologically similar to *Y. longissimum*, especially in leaf shape, but bearing short, fusiform gemmae (Fig. 6i–j), became sister to these two clades; these three clades were monophyletic with high support values (100/100, and 1.0).

Discussion

Circumscription of the Pylaisiadelphaceae and Sematophyllaceae

Sematophyllaceae are an old family first established by Brotherus (1905) in the first edition

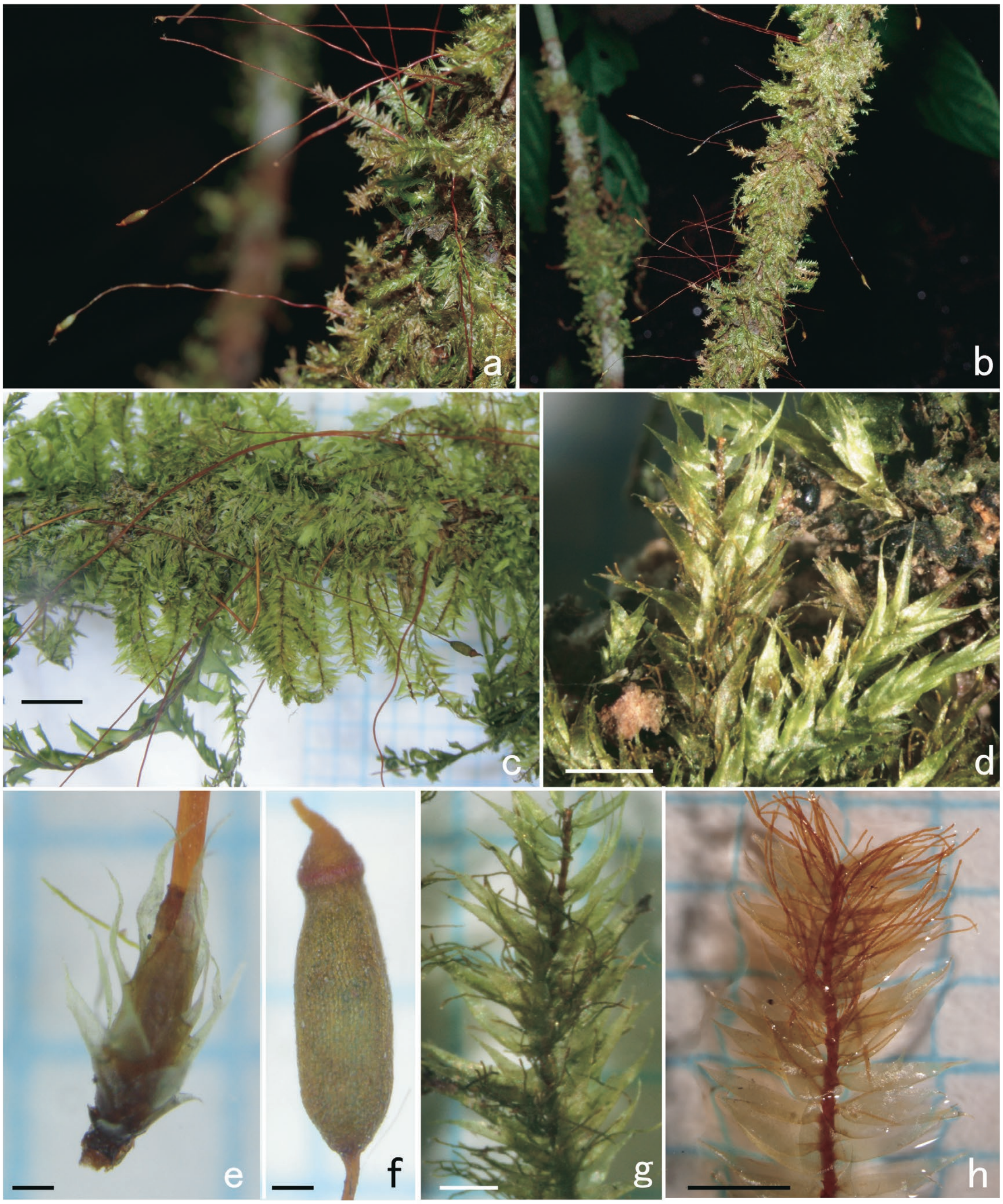

FIG. 3. *Orientobryum oligonema* (1). a & b: Plants with sporophytes. c: Closeup of stems and branches with sporophytes. d: Closeup of upper part of branches with a number of gemmae. e: Vaginula with perichaetial leaves. f: Capsule. g (dry) and h (wet): Branches with filamentous gemmae. Scales = 2 mm for c; 1 mm for d & h; 0.2 mm for e & f; 0.5 mm for g. All from *H. Akiyama 24086*.

of "Die Natürlichen Pflanzenfamilien" 1(3) (p. 706). Recent molecular studies using *rbcL* sequences revealed its paraphyletic affinity (Tsubota *et al.* 2000, 2001a, b). Goffinet & Buck (2004) created a new family, the Pylaisiadelphaceae, to accommodate 16 genera (now 15 genera because

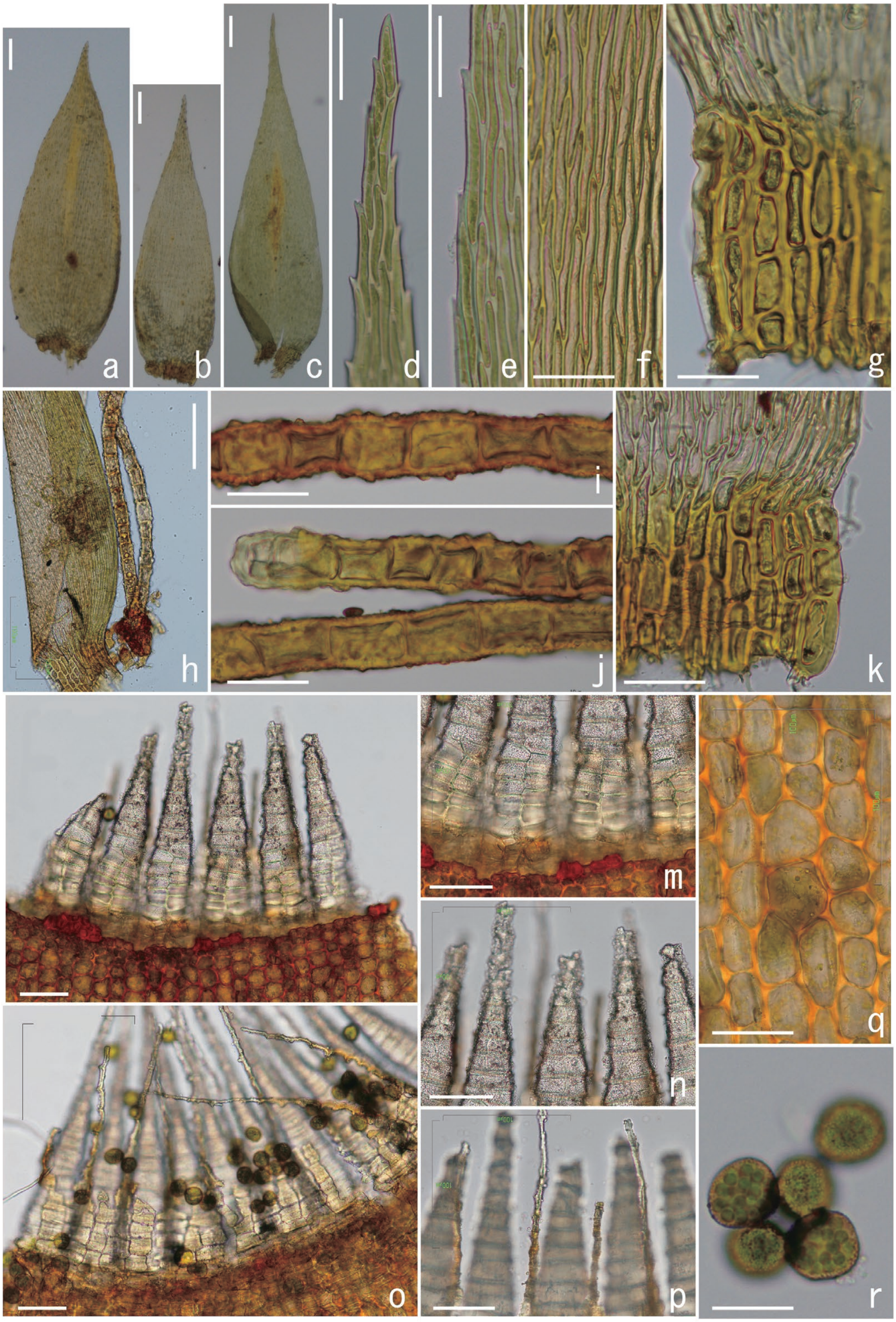

FIG. 4. *Orientobryum oligonema* (2). a–c: Branch leaves. d: Apex of a branch leaf. e: Upper margin of a branch leaf. f: Upper laminal cells of branch leaf. g: Alar of a branch leaf. h: Branch leaf and subtended filamentous gemmae. i & j: Closeup of gemmae with mammillose cells. k: Closeup of alar cells of branch leaf. l: Outer surface of exostome teeth. m: Basal part of exostome teeth. n: Upper part of exostome teeth. o: Inner surface of endostome with low basal membrane, filamentous segments and short cilia. p: Upper part of segments. q: Exothecial cells. r: Spores. Scales = 100 µm for a–c and h; 40 µm for others. All from H. *Akiyama 24086*.

Aptychella and *Clastobryopsis* are synonymous; Akiyama *et al.* 2015) segregated from the Sematophyllaceae *s. lat.* They defined the family by the following morphological features; (1) exothecial cells not collenchymatous, (2) alar cells smaller and mostly not inflated, and (3) pseudoparaphyllia often filamentous. Goffinet *et al.* (2009) followed this treatment. Later, Cox *et al.* (2010), using plural DNA markers (*rps4*, *nad5* and *nc26S*), indicated the paraphyly of Pylaisiadelphaceae and some genera (*Mastopoma*, *Heterophyllium*, and *Pseudotrismegistia* along with *Wijkia* and *Isocladiella*) closely related to members of the Sematophyllaceae *s. str.* Huttunen *et al.* (2012) showed monophyly of the Pylaisiadelphaceae and its sister relationship to the Sematophyllaceae, but they included only three genera (*Brotherella*, *Isopterygium*, and *Taxithelium*) from the Pylaisiadelphaceae in their analysis, and these genera are core members of the Pylaisiadelphaceae *s. str.* In the present study, 12 of the 15 genera (*Platygyrium*, *Pterogonidium*, and *Taxitheliella* are missing) in the family were included. Their inclusion suggests that both Pylaisiadelphaceae *s. lat* and Heterophyllioideae are paraphyletic. In addition, it became clear that three monophyletic clades are in the Sematophyllaceae *s. lat.*: they are (1) Pylaisiadelphaceae *s. str.*, (2) *Clastobryum*, and (3) Sematophyllaceae *s. str.* + Heterophyllioideae. For Sematophyllaceae *s. str.* (Goffinet & Buck 2004, Goffinet *et al.* 2009), although only 5 out of 28 genera were included in the present analyses, they form a well supported monophyletic clade. The results agree well with the phylogenetic tree indicated in Cox *et al.* (2010), except for the *Clastobryum* clade, which was not included in their analysis. As for subfamily Wijkioideae with three genera (*Acanthorrhynchium*, *Trismegistia*, and *Wijkia*) proposed by Hedenäs & Buck (1999) in place of the Heterophyllioideae, it was not supported in the present analyses.

Clastobryum (except for *C. oligonema*) was phylogenetically analyzed with molecular markers for the first time in the present study. It has long been classified in the Sematophyllaceae, but Goffinet & Buck (2004) and Goffinet *et al.* (2009) placed it in the Pylaisiadelphaceae. The present results suggest that it is in a clade with all the members of the Sematophyllaceae and Pylaisiadelphaceae, but its systematic position is left ambiguous because ML/MP and BI analyses suggest different results. It is notable that *Clastobryum* has distinct alar cell formations (large, thick walled, highly bulging, deeply colored and arranged in a single row at the bottom of the alar regions), which are unique among pleurocarpous mosses. Such features are shared only by the members of the genus *Acroporium*. Since *Acroporium* is a member of Sematophyllaceae *s. str.*, morphological resemblance in alar structure might be due to convergence.

Re-examination of the taxonomic status of Yakushimabryum

Yakushimabryum was first established by Akiyama *et al.* (2011) based on a phylogenetic analysis using *rbcL* sequences as well as on external morphology, such as smooth and long rectangular cells of filamentous gemmae and entire basal leaf margins. Although Suzuki *et al.* (2013) treated *Y. longissimum*, the type species of the genus, as a synonym of *Gammiella tonkinensis*, Akiyama (2014) pointed out that the two species differ in the shape of the lower leaf margins and filamentous gemmae. The present results not only confirm that *Y. longissimum* and *G. tonkinensis* are separate species but suggest that they are closely related to each other and belong to the same genus. In additions, *G. pterogonioides* and *Aptychella proligera*, which are the type species of the genus *Gammiella* and *Aptychella*, respectively, were revealed to be distantly related to both (1) *G. tonkinensis* and (2) *G. touwii* and *A. subintegra* in the clade of *Y. longissimum.*

Judging from habitat preferences and an examination of the type specimen of *Gammiella touwii*, it revealed itself to be an ecotype of *Yakushimabryum longissimum*, growing in rather windy places and having only long, pendulous branches in place of normal short branches. Additional evidence is that even typical plants of *Y. longissimum*, when growing on the branches of shrubs at the edge of the forest floor or in rather open places along mountain ridges, often develop long, pendulous, slender flagelliform branches at the tips of branches, as in *Gammiella touwii.* In addition, filamentous gemmae are present in the leaf axils on normal branches and absent from pendulous branches of *Yakushimabryum longissimum*. Since *G. touwii* is composed of only pendulous branches, which thus may be the reason *G. touwii* lacks gemmae. Terminal portions of such pendulous branches of *G. touwii* are often fragile and broken fragments can serve as asexual reproductive organs.

Aptychella is composed of around ten species (Akiyama *et al*. 2015, Akiyama 2016). Most species are in East and Southeast Asia but a single species, *A. proligera*, has been reported from only Central and South America. Akiyama *et al.* (2015) demonstrated the monophyly of the genus and treated the *Clastobryopsis* M. Fleisch. as a synonym of *Aptychella*. Although only five species were included in the present study, the monophyly of the genus is again confirmed by the present larger-scale molecular analyses with many additional taxa from the Pylaisiadelphaceae and Sematophyllaceae. In addition, *A. subintegra* is revealed to be distantly related to members of the *Aptychella*, but with close affinities to *Y. longissimum* and *Gammiella touwii.*

As a result, *Gammiella touwii*, *Aptychella subintegra*, and *Yakushimabryum longissimum* are confirmed as belonging to a single species. The oldest name available is *Y. subintegrum*. *Gammiella tonkinensis* should be treated as a member of *Yakushimabryum* under the name *Y. tonkinensis*. In addition, a new species, *Y. brevigemmium* H. Akiyama (described below) is proposed on the basis of its morphology and the results of the phylogenetic analyses. The taxonomic treatment for these species is summarized below with descriptions and notes for each species. It is also notable that recognizing these three species in the genus *Yakushimabryum* means that there are three different types of asexual gemmae in the genus; (1) filamentous gemmae with smooth, long rectangular cells in *Y. subintegrum* (Fig. 6, s–z), though there is a slight difference in two Taiwanese plants (Fig. 6m–r), (2) filamentous gemmae with short, mammillose, rectangular cells in *Y. tonkinensis* (Fig. 6a–l), and (3) short, fusiform gemmae with smooth, short rectangular cells in *Y. brevigemmium* (Fig. 5i & j).

Taxonomic status of Clastobryum oligonema *and its relationship to the BPW clade*

After examining the types and other authentic specimens of the species formerly identified as members of *Clastobryum* from South and East Asia, it became clear that *Gammiella tonkinensis* has been confused with various species of *Clastobryum*, mainly because of the similar morphology of their asexual reproductive organs; they share filamentous gemmae with short rectangular, more or less mammillose (or papillose) cells borne in the leaf axils. Among the species, *Clastobryum oligonema* is one of the representatives distributed in southern India and Indochina. In the present analyses, the seven samples of the species from northern Thailand and northern, central, and southern Vietnam formed a monophyletic clade. The clade, however, was not closely related to *G. tonkinensis* nor to the other three species of *Clastobryum* (*C. glabrescens*, *G. scalare*, and *G. spiculiferum*) examined. In addition, among the seven samples of *C. oligonema*, one is distantly related to the other six. Judging from their morphology (Figs. 3–5) and from the phylogenetic results, I treat them as representing two separate species. Both species share filamentous gemmae with mammillate cells emerging from alar cells, and scalariform alar formation.

There have been two contradictory opinions on the relationships between *Brotherella* and *Pylaisiadelpha.* Buck (1984) treated both genera as synonymous, while Ando *et al.* (1989) retained them as distinct genera. Later, using *rbcL* sequences, Tsubota *et al.* (2001) pointed out the polyphyletic nature of both *Brotherella* and *Wijkia.* It is notable that in the present analyses, three genes sequences support *Brotherella henonii*, *B. recurvans*, *Pylaisiadelpha tenuirostris*, *P. tristo-viride*, *Wijkia deflexifolia*, and *W. hornschuchii* as forming a monophyletic clade [*Brotherella-Pylaisiadelpha-Wijkia* (BPW) clade; Tsubota *et al.* 2001a]. It is also suggested from the

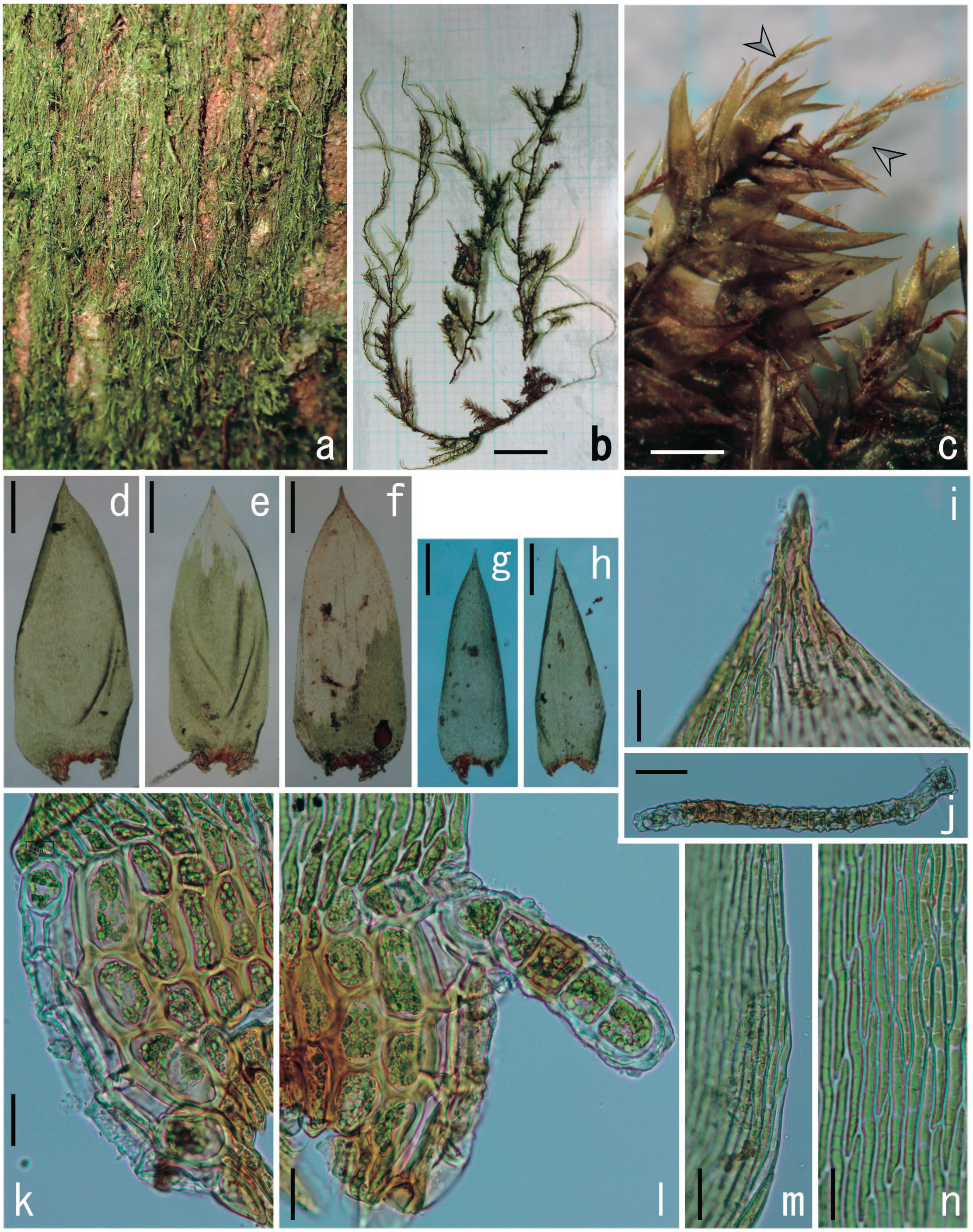

FIG. 5. *Orientobryum ovalifolium*. a: Habitat on tree trunk. b: Plants in dry condition. c: Deciduous branchlets (arrow heads) at branch apex. d–f: Secondary stem leaves. g & h: Branch leaves. i: Apex of a secondary stem leaf. i: Filamentous gemma. k: Alar of a secondary stem leaf. l: ditto. bearing a filamentous gemma from an alar cell. m: Margin of a secondary stem leaf. n: Median laminal cells of a secondary stem leaf. Scales = 5 mm for b, 0.5 mm for c, 0.2 mm for d–h, 40 µm for i, and 20 µm for others. All from the holotype (*H. Akiyama 24006*).

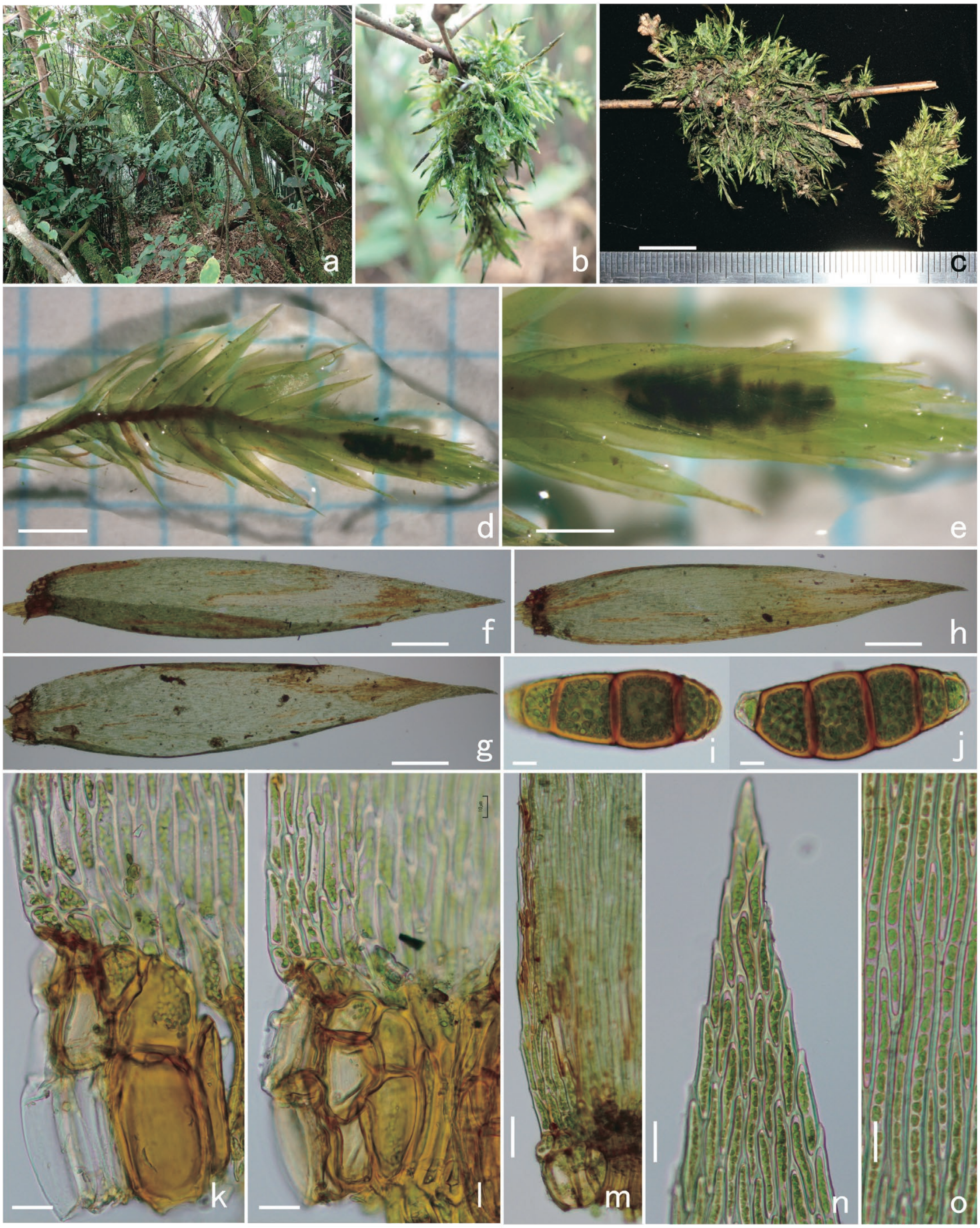

FIG. 6. *Yakushimabryum brevigemmium*. a–c: Habitat. d & e (Closeup): Wet branch with short gemmae in leaf axils. f–h: Branch leaves. i–j: Gemmae. k–l: Alar regions of branch leaves. m: Alar cells of slender leaf bearing gemmae in axil. n: Apex of a branch leaf. o: Median laminal cells. Scales = 1 mm for c & d; 0.5 mm for e; 0.2 mm for f-h; 10 µm for i & j; for 20 µm for k-o. All from the type (*H. Akiyama 24142*).

trees (Figs. 1 & 2) that (1) the members of the BPW clade and (2) seven samples of *Clastobryum oligonema* form two separate monophyletic clades. The phylogenetic relationships of these two clades remains ambiguous, although the BI analysis supports their close affinity. *Clastobryum oligonema* was first described by Cardot & Potier de la Varde in Potier de la Varde (1923) as a new species of *Clastobryum*. In those days the generic concept of *Clastobryum* was different from that of the present and was usually recognized in a much wider sense. Thus the genus had been regarded as including *Aptychella*, *Clastobryopsis*, *Clastobryophilum*, and *Gammiella*, which are now treated as separate genera. However, *Clastobryum* is now defined to include species with bulging, thick walled, red alar cells that are arranged in a single row and often reaching the median leaf base (Iwatsuki 1977, Tan & Buck 1989, Tan & Iwatsuki 1992). Alar cells of *C. oligonema* are differently arranged from those of other species of *Clastobryum*; they are evenly thick walled, pale brown, short to long rectangular, and arranged in a scalariform manner (Fig. 4 g, k, & Fig. 5 k, l), all features common in the Pylaisiadelphaceae. In addition, the present molecular analyses indicated a distant relationship of the three species of *Clastobryum* (*C. glabrescens*, *C. scalare*, and *C. spiculiferum*) from *C. oligonema*. On the other hand, judging from the molecular analyses and similarities in external morphology, *Aptychella*, *Gammiella*, *Isocladiella*, *Isopterygium*, and *Yakushimabryum* are close relatives to *C. oligonema*. As a result, I propose to establish a new genus, *Orientobryum* H. Akiyama, to accommodate *C. oligonema* as *O. oligonema* along with a new species, *O. ovalifolium*, in the Pylaisiadelphaceae.

Taxonomic treatment

1. **Orientobryum** H. Akiyama, **gen. nov.** (Pylaisiadelphaceae)

Similar to *Pylaisiadelpha* and *Yakushimabryum* in appearance, leaf shape, and alar formation with short to long rectangular cells arranged in a scalariform manner, but differing in strongly mammillose, long, filamentous gemmae emerging from alar cells, long setae, and a double peristome with lanceolate exostome teeth and filamentous cilia.

Typus. Orientobryum oligonema (Cardot & P. de la Varde) H. Akiyama.

Description. Primary stems long creeping on substrate, pinnately branched. Branches (secondary stems) usually to 1 cm long, more or less complanately foliate. Upper portions of branches sometimes becoming flagelliform and long pendent (for example, *He & Nguyen 42616* and *42611*, both MO, collected in central Vietnam). Filamentous gemmae emerging from alar cells and situated in leaf axils, the brown color contrasting well with the green leaves. Cells of gemmae short rectangular, ca. 25 × 20 μm, thick walled, densely mammillose.

Key to the species

1a. Filamentous gemmae more than 1.5 mm long, if not broken; caducous branchlets absent .... 1-1. *O. oligonema*
1b. Filamentous gemmae less than 0.9 mm long; caducous branchlets present .... 1-2. *O. ovalifolium*

1-1. **Orientobryum oligonema** (Cardot & P. de la Varde) H. Akiyama, **comb. nov.** — Figs. 3 & 4

Basionym: *Clastobryum oligonema* Cardot & P. de la Varde in Potier de la Varde, Revue Bryologique 50: 74 (1923), erroneously synonymized under *Aptychella tenuiramea* (Mitt.) P. Tixier by Tixier (1977). —Type: South India, Madura, Kodaikanal, 1911, *R. Foreau 74* [holo- (PC0147649) & iso- (PC0701623) in PC!].

Clastobryum barbelloides Dixon & P. de la Varde, Archives de Botanique, Bulletin Mensuel 1(8–9): 174 (1927), erroneously synonymized under *Aptychella tenuiramea* by Tixier (1977). —Type: South India, Palni Hills, Old Ghat Road, Shembaganur, 22 Jan. 1927, *R. Foreau 656* (holo- in BM!).

Chionostomum angustifolium Dixon, Annales Bryologici 9: 70 (1937), erroneously synonymized under *Aptychella tenuiramea* by Tixier (1977). —Type: Laos, Pu Mutên, Chieng-kwang, c. 1500 m, 20 Apr. 1932, *A. F. G. Kerr 514* (holo- in BM!).

Plants forming low turf, light green or yellowish green, more or less shiny. Primary stems creeping on substrate, densely branched. Secondary stems (branches) usually 1–2 cm long, spreading horizontally, sparsely branched especially in upper portions, sometime becoming terete and long pendulous (to 5 cm long); 0.1 mm in diameter without leaves, central strand absent; distinctly complanate-foliate, penicilate at apex. Paraphyllia absent. Pseudoparaphyllia short filamentous to narrowly triangular. Gemmae frequent, filamentous, reaching 1.5 mm long (often longer than leaf), conspicuous even without magnification, formed in leaf axils except for basal portions of secondary stems, greenish but soon turning reddish brown; cells quadrate to short rectangular, thick walled, densely mammillate. Axillary hairs 150–180 µm long, 3–4-celled; three long and colorless cells above with a single rectangular slightly brownish base cell. Rhizoids pale brown, smooth. Leaves ovate to widely ovate (lanceolate on pendulous slender branches), gradually narrowed into long acuminate apex, 0.9–1.5 mm long, 0.3–0.45 mm wide, not decurrent at base; ecostate; margins plane, distantly serrulate apically, sparsely but clearly denticulate basally; alar cells well differentiated, scalariform in arrangement. Upper laminal cells smooth, rhomboidal, 25–40 µm long, ca. 3 µm wide, thin walled; median laminal cells smooth, linear, 70–90 µm long, ca. 3 µm wide, thin walled; central basal cells long rectangular, thick walled, more or less porose; alar cells quadrate to short to long rectangular, thick walled, colored.

Dioicous. Male organs not observed. Perichaetia terminal on short lateral branches of primary stems; archegonia ca. 20 in number; with numerous paraphyses and several linear-lanceolate, leaf-like scales. Perichaetial leaves linear-lanceolate, to 1.6 mm long, narrowly long acuminate, ecostate; alar cells differentiated. Inner post-fertilization perichaetial leaves lanceolate, narrowly long acuminate, to 2.5 mm long, ecostate. Vaginula slightly developed, to 1 mm long. Calyptrae cucullate, smooth, naked.

Setae ca. 20–30 mm long, yellow when young, soon turning reddish brown, smooth. Capsules cylindrical, straight, 1.2–2 mm long; exothecial cells smooth, strongly collenchymatous. Operculum conical, to 0.5–0.8 mm long with slightly inclined short beaks. Peristome double. Exostome teeth pale white or slightly brownish, lanceolate, 250–300 µm long, finely papillose, with zigzag central lines, not perforate at all. Endostome segments filamentous, as long as exostome teeth; basal membranes ca. 80 µm long, mostly smooth; cilia short, 1–2 cells long, papillose. Spores green, spherical, 30–40 µm long, minutely and finely papillose.

Habitat. *Orientobryum oligonema* forms compact and low tufts on branches of undergrowth at the forest floor in well-preserved, evergreen montane forests. It is not rare and sometimes is locally abundant, for example, at 1,700 m elev. in Doi Inthanon, northern Thailand, at 1,600 m elev. in southern Vietnam, and at 1,000 m elev., in northern Vietnam. It often grows on the upper side of horizontally spreading branches of shrubs and short trees.

Distribution. China, India, Laos, Sri Lanka, Thailand, Vietnam.

Other specimens examined. **THAILAND.** Chiang Mai Co., Doi Inthanon, 15 ha Permanent Plot, near Check Point 2, 18°31'34" N, 98°24'47" E, ca. 1650 m elev., *H. Akiyama*, *M. Kanzaki*, *T. Irie & N. Ando 21*, *113*, *116* (with sporophytes), *151*, *171*, *172*, *202* (with sporophytes), *251*, *252* (with sporophytes), *341*, *384*, and *405* (with sporophytes) (all HYO!); near Doi Ang Ka Noi Village, 1300 m elev., *M. Kanzaki & T. Irie 001* (HYO!); ibid., *H. Akiyama & N. Printarakul 1431* (HYO!). **VIETNAM.** Lam Dong, Bidoup Nui-Ba National Park, behind Hon Gao Station, Dec. 11, 2012, *T. T. Luong 1210-039* (HYO!, SING); ibid., in the vicinity of Hon Giao Forest Station, 12°11'02" N, 108°42'88" E, 1560 m elev., Nov. 13, 2014, *H. Akiyama 23982* (HYO, PHH, VNM); Da Nang, Hoa Vang District, Hoa Ninh Commune, Ba Na-Nui Chua Natural Reserve, 15°59'51" N, 107°59'08" E, 1440 m elev., April 7, 2010, *Si He & Khang Nguyen 42623* (DNA voucher), *42611*, *42616* (DNA voucher) & *42662* (all MO!; as *Gammiella tonkinensis*); Vinh Phuc Co., Tam Dao National Park, in the vicinity of the Lodge Housem, 21°28'23" N, 105°38'22" E, 970 m elev., Nov. 17, 2015, *H. Akiyama 24086* (DNA voucher) & *24129* (both HYO, PHH, VNM); ibid., Tam Dao City, approach to the Television Tower Mountain, 21°28' N, 105°38' E, 1210 m elev., Nov. 19, 2014, *H. Akiyama 24133* (HYO, VNM); ibid., 1210 m elev., *H. Akiyama 24183* (HYO, PHH, VNM; DNA voucher); ibid., around the Lodge House, 21°28'23" N, 105°38'22" E, 980

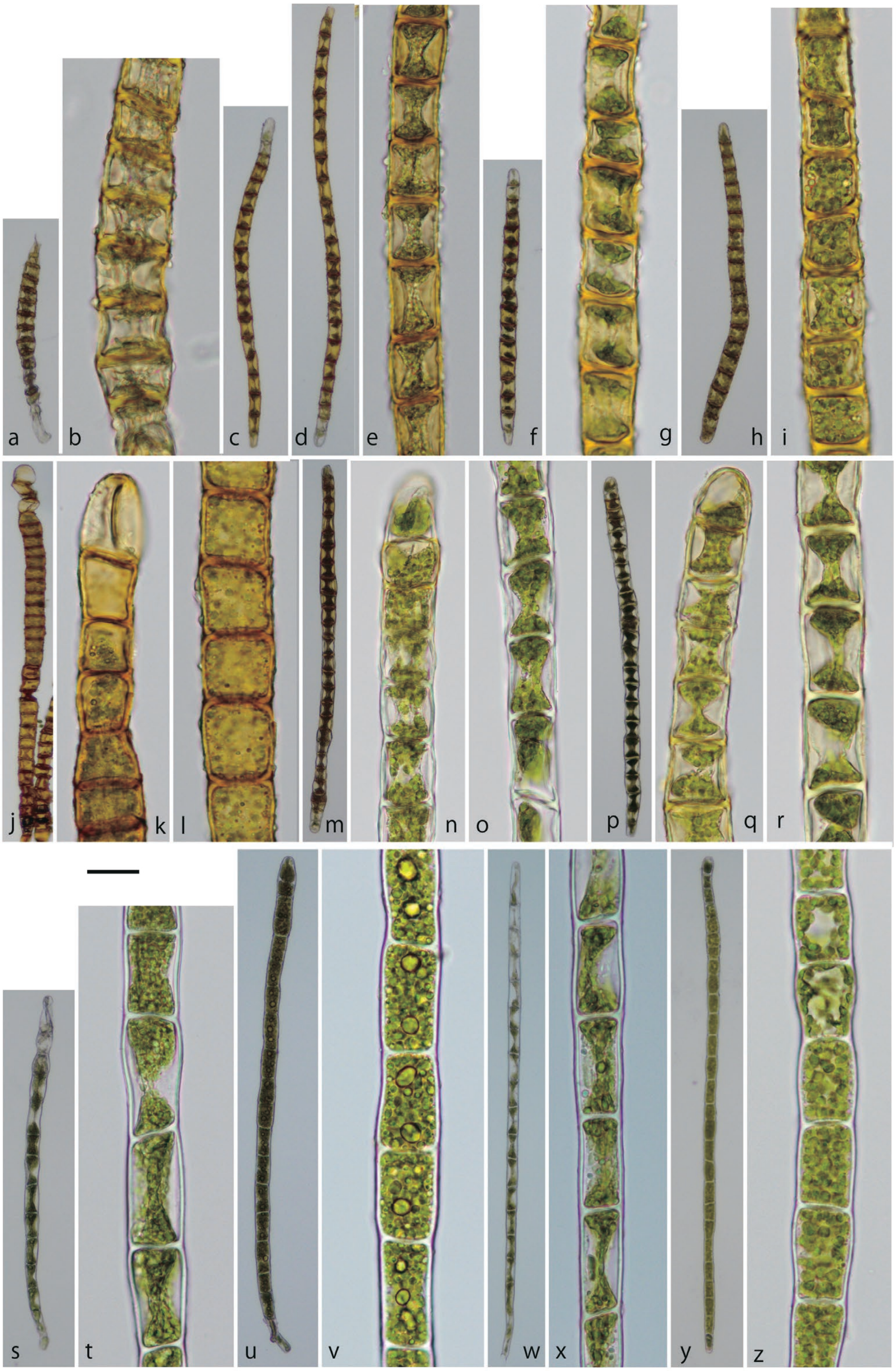

FIG. 7. Variation in filamentous gemmae of *Yakushimabryum tonkinense* (a–l) and *Y. subintegrum* (m–z). a & b: holotype of *Clastobryum tonkinense*. c–e: Japan, Nara Pref., *Kimura 8339*. f & g: Japan, Miyazaki Pref., *Akiyama 22942*. h & i: Vietnam, Tam Dao, *Akiyama 24161*. j–l: Taiwan, Taoyuan, *Akiyama 24296*. m–o: Taiwan, Taichung, *Akiyama 23284*. p–r: Taiwan, Tai'an, *Akiyama 24132-b*. s & t: Japan, Hachijyo, *Akiyama 22802*. u & v: Japan, Yakushima, *Akiyama 22777*. w & x: Japan, Miyazaki, *Akiyama 22942*. y & z: Vietnam, Tam Dao, *Akiyama 24161*. Scales = 0.1 mm for a, c, d, f, h, j, m, p, s, u, w and y; 20 µm for b, e, g, i, k, l, n, o, q, r, t, v, x and z.

m elev., Nov. 19, 2014, *H. Akiyama 24151*, *24153* and *24154* (all HYO, PHH, VNM). **LAOS.** Holotype of *Chionostomum angustifolium*. **CHINA.** Hainan Prov., Ledong Co., Jianfengling National Nature Reserve, Jianfengling, 18°42.589' N, 108°52.590' E, 1215 m elev., Sept. 27, 2006, *L. Zhang 5182* (SING!, SZG; as *Clastobryopsis planula*). **INDIA.** Tamil Nadu Prov., Palni Hills, upper part of Perumalmalai Shola, ca. 6500 ft. elev., 5 Apr. 1926, *G. Foreau 228* (paratype of *Clastobryum barbelloides*, BM). **SRI LANKA.** NNW of Kandy, Top of Hunnasgiriya, 24 Nov. 1929, *Galston 2579* (BM).

Note 1. Distinguishing features of *Orientobryum oligonema* are as follows: (1) Branch leaves widely spreading in wet and dry conditions, arranged in eight ranks but more or less complanate; (2) branch tips sometimes becoming flagelliform and the whole plant becoming long pendulous; (3) branch leaves long acuminate; (4) filamentous gemmae abundant, often longer than surrounding leaves, fragile; young gemmae green and resembling green algae; cells strongly mammillose, short rectangular; (5) capsules long cylindrical; (6) exostome teeth not perforate, and (7) exothecial cells collenchymatous.

Note 2. Orientobryum oligonema is quite similar to *Yakushimabryum tonkinense* (≡ *Gammiella tonkinensis*) in general appearance. A number of herbarium specimens have been misidentified as such. It is true that *O. oligonema* and *Y. tonkinense* share narrowly lanceolate leaves with distinct serration on the lower margins and mammillose filamentous gemmae. This is probably the main reason why *C. oligonema* has not been recognized [for example, see He & Nguyen (2012)]. Previous reports of *Y. tonkinense* (as *G. tonkinensis*) in various local floras and checklists of East and Southeast Asian regions should be carefully re-examined.

The long acuminate apex of the branch leaves and the more or less uneven alar cell size in *Orientobryum oligonema* are good features to distinguish the species from *Y. tonkinense*, which has acute leaves and mostly short rectangular alar cells. These two species also differ in the length of the filamentous gemmae; usually more than 1.5 mm long in *O. oligonema* versus 0.4–1.2 mm long in *Y. tonkinense*. Most plants of both species bear abundant gemmae at all seasons and thus long filamentous gemmae of the former species are useful for distinguishing the two species in the field.

Note 3. Orientobryum oligonema shares straight lanceolate branch leaves, and straight and cylindrical capsules on long setae with *Pylaisiadelpha tenuirostris* and *Yakushimabryum subintegrum* (≡ *Y. longissimum*), but they do not form a monophyletic clade (Fig. 1 & 2).

Note 4. Tixier (1977) treated *Orientobryum oligonema* (as *Clastobryum oligonema*) as a synonym of *Aptychella tenuiramea* without supporting evidence. As pointed out by Tan (1990) and Arikawa (2004), *A. tenuiramea* has a close affinity with *Brotherella* Loeske *ex* M.Fleisch. judging from the alar morphology. Therefore, I do not follow the treatment proposed by Tixier (1977).

The plants reported from northern Vietnam by Tran Ninh (1993, p. 579) and those from South India by Daniels (2010, p. 36) under the name of *Aptychella tenuiramea* probably are *Orientobryum oligonema.* Such misidentifications are based on the treatment proposed by Tixier (1977), who erroneously synonymized *Clastobryum oligonema*, *C. barbelloides*, and *Chionostomum angustifolium* under *Aptychella tenuiramea.*

Note 5. Three specimens collected in central Vietnam (*He & Nguyen 42562*, *42611* and *42626* deposited in MO) have quite slender, pendulous secondary stems. In addition, they are strongly shinier in comparison with those from other localities. Other morphological features, as well as DNA sequences, however, agree well with those of typical *Orientobryum oligonema.* Similar morphological variation is also observed in *Yakushimabryum subintegrum* (note 1).

1-2. **Orientobryum ovalifolium** H. Akiyama, **sp. nov.** —Fig. 5

Closely related to *Orientobryum oligonema*, but differing in pendent stems, shorter filamentous gemmae, presence of caducous branchlets, ovate and shallowly concave leaves with entire to only minutely serrulate margins.

Typus. **VIETNAM.** Lam Dong, Bidoup-Nui Ba National Park, in the vicinity of Giang Ly Forest Station, 12°10'52" N, 108°41'01" E, 1460 m elev., Nov. 13, 2014, *H.*

Akiyama 24006 (holo- in HYO, iso- in BM, L, NY, PHH, VNM).

Plants light green, more or less shiny, forming thin carpets on tree trunks. Primary stems short, creeping, densely branched. Secondary stems creeping and appressed to substrate, 3–5 cm long, irregularly pinnately branched, often becoming flagelliform at apex, complanately foliate, ca. 0.1 mm in diameter without leaves; central strand absent. Branches 4–12 mm long, complanately foliate. Paraphyllia absent. Pseudoparaphyllia short filamentous to narrowly triangular. Gemmae few, filamentous, 0.1–0.3 mm long, emerging from alar cells; cells quadrate to short rectangular, thick walled, densely mammillate. Caducous branchlets present on upper part of branches. Axillary hairs 120–180 μm long, 3- or 4-celled; three long, colorless cells above with a single rectangular slightly brownish base cell. Rhizoids pale brown, smooth. Secondary stem leaves shallowly concave, ovate (lanceolate on pendulous slender branches), abruptly narrowed into short apex, gradually narrowed into long acuminate apex, 1–1.5 mm long, 0.4 mm wide, more or less cordate at base but not decurrent; ecostate; margins plane, finely serrulate apically, minutely serrulate or almost entire basally; alars well differentiated, scalariform in cell arrangement. Branch leaves shorter than stem leaves, to 0.8 mm long, lanceolate; margins widely inrolled. Upper laminal cells smooth, rhomboidal, 25–40 μm long, ca. 3 μm wide, thin walled; median laminal cells smooth, linear, 60–100 μm long, ca. 3 μm wide, thin walled; central basal cells long rectangular, thick walled, more or less porose; alar cells quadrate to short to long rectangular, thick walled, colored. Sexual organs and sporophyte not seen.

Habitat. Forming a thin carpet on tree trunks in rather dry montane evergreen forests, appearing similar to slender and pendulous species of *Acroporium* (Fig. 5, a & b).

Distribution. Southern Vietnam.

Other specimens examined. Only a single spcimen (type) is so far known.

Note. Orientobryum ovalifolium shares filamentous gemmae emerging from alar cells and scalariform alar cells with *O. oligonema*. Results from the DNA analysis suggest a close relationships between these two species. The former, however, differs from the latter in being pendulous, having more or less concave, ovate leaves, much shorter filamentous gemmae (0.1–0.3 mm long), only weakly or almost entire basal leaf margins, and caducous branchlets.

2. **Yakushimabryum** H. Akiyama, Y. Chang, T. Yamag. & B. C. Tan, Journal of Bryology 33(1): 42 (2011) (Pylaisiadelphaceae)

Type species: *Y. longissimum* H. Akiyama, Ying Chang, Yamaguchi & B.C. Tan.

Key to the species

1a. Gemmae short fusiform, composed of only 5 or 6 cells, 110–125 μm long .... 2-3. *Y. brevigemmium*
1b. Gemmae filamentous, composed of more than 15 cells, more than 300 μm long at maturity 2
2a. Basal leaf margins entire or minutely crenulate; cells of filamentous gemmae smooth, thin walled and longrectangular .... 2-1. *Y. subintegrum*
2b. Basal leaf margins distinctly serrulate; cells of filamentous gemmae mammillose, thick walled and short rectangular .... 2-2. *Y. tonkinense*

2-1. **Yakushimabryum subintegrum** (P. Tixier) H. Akiyama, **comb. nov.** —Fig. 7m–z.

Basionym: *Aptychella subintegra* P. Tixier, Revue Bryologique et Lichénologique 34: 160 (1966). —Type: Vietnam, Tam Dao, 950 m, 7 Juin 1926, V. Demange 280 (holo- Herb. R. Henry, in PC!).

Gammiella touwii B.C. Tan, Bryologist 93: 432 (1990), erroneously synonymized under *Gammiella tonkinensis* (Tan & Yu 1999). —Type: Philippines, Mindanao, Bukidnon Prov., Mt. Kitanglad, on log, ca. 1800 m, 25 May 1984, *Tan, Navarez & Amoroso 84-307* (holo- in FH!, iso- in BM, H, L, NICH!, NY).

Yakushimabryum longissimum H. Akiyama, Y. Chang, T. Yamag. & B.C. Tan, Journal of Bryology 33: 42 (2011), erroneously synonymized under *Gammiella tonkinensis* (Suzuki *et al.* 2013). —Type: Japan, Kagoshima Pref., Yakushima Island, en route from Yakusugi-land to Hananoego moor, 1070 m., *Akiyama 20318* (holo- in HYO!, iso- in HIRO!, NY!, SING!). For more details, see Akiyama (2014).

Plants rather glossy, green or yellowish green, older parts becoming brownish. Primary stems prostrate, attached tightly to substrate with rhizoid bundles, densely and irregularly branched. Secondary stems, if present, short, ascending, irregularly branched mostly at base. Branches mostly simple, ascending, to 20 mm long, more or less fragile especially upper portions, with distinct long and slender tips bearing narrower leaves; a few dormant buds present on upper portions, naked. Stems and branches without central strands, less than 0.1 mm in diameter; epidermal cells of branches long rectangular and evenly thick walled; small cell masses with thin walled, quadrate to short rectangular cells present on upper caudate portions from which filamentous gemmae emerge. Gemmae filamentous, pale green, 5 or 6 in each axil, consisting of short and smooth cells, tightly appressed to stems in leaf axils. Rhizoids reddish brown, in fascicles, sparsely papillose, mostly from lower surface of prostrate primary stems. Axillary hairs ca. 150 µm long, consisting of 4 smooth, transparent cells; basal single cell not much differentiated, but shorter and slightly colored. Paraphyllia and pseudoparaphyllia absent. Stem leaves ca. 1 mm long, widely spreading basally, ovate, acuminate; costa indistinct; margins crenulate apically, entire basally; laminal cells linear, slightly sinuate, smooth; alar cells quadrate, more or less colored, arranged in a scalariform manner. Leaves of lower portion of branches similar to stem leaves in shape, somewhat longer. Leaves of middle and upper portion of branches more or less appressed to stems, lanceolate, slightly narrowed at base, gradually narrowed to acuminate apex, 1.5–2 mm long, more or less concave basally; margins distinctly crenulate apically, plane; costa absent or short, single or bifid; laminal cells linear-fusiform, smooth, 80–100 µm long, ca. 3 µm wide, becoming shorter at apex, ca. 30 µm long; alar cells somewhat bulging, deep reddish brown (younger leaves pale green), quadrate to short rectangular, thick walled (outermost cells thin walled), not decurrent. Leaves at caudate tips becoming much narrower than those below.

Dioicous. Male plants similar both in size and branching pattern to female plants. Perichaetia on primary and secondary stems; with ca. 10–15 archegonia surrounded by a few paraphyses. Outermost perichaetial leaves ca. 0.7 mm long, ovate, rather abruptly narrowed into acuminate apex, ecostate; inner perichaetial leaves ca. 1.2 mm long, ecostate, narrowly lanceolate, gradually narrowed into apex. Perigonia on lateral short branches or at apex. Perigonia on ascending shoots, bud-like in appearance, with ca. 5–7 antheridia. Perigonial leaves broadly ovate, cuspidate, reddish brown basally, ecostate; alar region scarcely differentiated. Calyptrae cucullate, smooth, naked.

Setae 12–20 mm long, smooth, yellowish green when young, becoming reddish brown later. Capsules narrowly ovoid to cylindrical with slender opercula, 0.5–2 mm long, erect or slightly inclined, remaining partially green even after deoperculation, later becoming reddish brown, more or less constricted just below mouth after deoperculation; annulus not differentiated; opercula sharply oblique, falling with calyptra; exothecial cells rectangular to hexagonal, evenly thick walled, not collenchymatous; stomata superficial, restricted to apophysis, ca. 10–15 in number. Peristome double, alternate. Exostome teeth 16, pale white or slightly brownish, lanceolate, long acuminate (sometimes two teeth adnate on upper portion; Fig. 16 in Akiyama 2014), 250–330 µm long, not perforate, mostly smooth to densely papillose on both surfaces. Endostome segments pale yellowish white, linear, varying in length, 100–200 µm long, densely papillose; cilia absent; basal membrane low, 50–70 µm in height, finely papillose. Spores spherical, green, slightly thick walled, finely papillose, ca. 25–30 µm in diameter.

Habitat. On branches and trunks of shrubs in montane forests.

Distribution. China (Hong Kong), Japan, Malaysia (Pahang), Philippines (Mindanao), Taiwan, and Vietnam.

Other specimens examined. **VIETNAM. Lam Dong Co.,** Da Lat, Bidoup-Nui Ba National Park, in the vicinity of Giang Ly Station, 12°10'52.2" N, 108°41'01" E, 1470–1530 m elev., Nov. 12, 2014, *H. Akiyama 23938* (HYO, VNM); **Vinh Phuc Co.,** Tam Dao National Park, en route from the Lodge House (979 m elev.) to the summit of Mt. Tam Dao 1 (1365 m), 21°28' N, 105°38' E, 1050 m elev., Nov. 18, 2014, *H. Akiyama 24119* (HYO, PHH, VNM); ibid., en route from the Lodge House (979 m elev.) to the summit of Mt. Tam Dao 1 (1365 m), 1190 m elev., Nov. 18, 2014, *H. Akiyama 24127* (HYO, PHH, VNM); ibid., Mt. Tam Dao, 21°27'36" N, 105°38'29" E, 900–1000 m elev., July 17, 2007, *P.S. Câmara 1675* & *1772* (both MO as *Gammiella tonkinensis*). **MALAYSIA. Pahang,** Cameron Highland, around the top of G. Brinchang, 1982 m elev., Apr. 6, 2012, *B.C. Ho 12-230* (HYO, KUL, SING as *G. tonkinensis*); ibid., Oct. 26, 2014, *H. Akiyama 23878* & *23913* (both HYO). **PHILIPPINES. Mindanao**, Bukidnon Prov., Mt. Kitanglad, on log, ca. 1800 m elev., 25 May 1984, *Tan, Navarez & Amoroso 84-307* (type of *Gammiella touwii*). **CHINA. Hong Kong,** Tai Mo Shan, 885 m elev., July 30, 1998, *Zhang Li 1352* (HKU, IBSC, KFBG, SINU!; with sporophytes intermingled with *Aptychella brevinervis*); ibid., 900 m elev., 25 May, 1998, *Zhang Li 1120* (IBSC, HKU, KFBG, SINU!). **TAIWAN. Miaoli Co.,** Tai'an Township, Hshuepa National Park, Syuejin Recreation Area, around the Visitor center, 1870 m elev., Oct. 8, 2013, *H.Akiyama 23153-b* (HYO). **Taichung City,** Heping Dist., Dasyueshan National Forest Recreation Area, along a trail between Police Station and Small Sacred Tree, 2200 m elev., Oct. 10, 2013, *H.Akiyama 23284* (HYO). **JAPAN. Tokyo Metor.,** Mikurajima, Mikurajima-mura, Oyama – Suzuhara moor, 800 m elev., Dec. 8, 2000, *M. Higuchi 37516* & *37498* (both TNS, as *G. tonkinensis*); ibid., Suzuhara moor – peak of Oyama, 760 m elev., Dec. 8, 2000, N. *Nishimura 10820* (TNS, as *G. tonkinensis*); ibid., peak of Mt. Nagataki-yama – Miyoga-ike, 790 m als., Dec. 9, 2000, *N. Nishimura 10888* (TNS, as *G. tonkinensis*); ibid., Sato –Oyama, 640 m als., July 14, 1981, *N. Nishimura 8096a* (TNS, as *G. tonkinensis*); ibid., 650 m elev., July 14, 1981, *M. Higuchi 10317a* (TNS, as *G. tonkinensis*). Hachijyo-cho, Hachijyoshima, Nishiyama (Hachijyo-Fuji), old crater, 790 m elev., Jan. 6, 1999, *H. Kiguchi 16973* (NICH, as *Aptychella tonkinensis*); ibid., 820 m elev., March 15, 2013, *H. Akiyama 22786* (HYO); ibid., 690 m elev., *Akiyama 22802* (HYO); ibid., Miharayama, 690 m elev., March 16, 2013, *H. Akiyama 22834* (HYO). **Kagoshima Pref.,** Osumi Peninsular, Kanoya-shi, northern slope and around the summit of Mt. Uodake, 740–940 m elev., Feb. 19, 2014, *H.Akiyama 23344*, *23356*, *23357*, *23358*, *23359* & *23360* (all HYO); ibid., eastern slope of Mt. Uodake, 740–835 m elev., July 12, 2014, *H. Akiyama 23759*, *23760*, *23762*, *23764* & *23766* (all HYO); Kinko-cho, en route from the visitor center to Mt. Inebitake (along the western trail), 845–960 m elev., July 13, 2014, *H. Akiyama 23771*, *23774*, *23777*, *23778*, *23782*, *23788* & *23800* (all HYO); Yakushima, Yakushima-cho, Shiratani-unsuikyo, ca. 850 m elev., March 6, 2013, *H.Akiyama 22774* (with sporophytes; HYO, NY) & *22777* (HYO); Yakushima, upper stream of Arakawa river, ca. 1230 m elev., March 5, 2013, *H.Akiyama 22750* (male + sporophytes; HYO), *22751* (with sporophytes; HYO, NY), *22757* (with sporophytes; HYO), *22766* (with sporophytes; HYO), *22768* (with sporophytes; HYO) & *22755* (with sporophytes; HYO); ibid., Kosugidani, in the vicinity of an arbor, 660 m elev., Apr. 16, 2013, *N. Hayashida s.n.* (HYO); ibid., Yakusugi-land, *H. Deguchi 34995* (HIRO, as *Aptychella glomerato-propagulifera*, voucher for AB051217); Amamioshima, Uken-mura, Mt. Yuwan, ca. 670 m elev., Jan. 13, 2016, *H. Akiyama 24382*, *24383*, and *24386* (all HYO); ibid., around the summit, 695 m elev., Jan. 13, 2016, *H. Akiyama 24471* (HYO); ibid., 600–694 m elev., Dec. 4, 1988, *H. Deguchi 32197* (HIRO, TNS; as *Aptychella glomerato-propagulifera* and *Gammiella tonkinensis*); Tokunoshima, Tokunoshima-cho, Mt. Inokawa-dake, Ohara-route, 540–645 m elev., Jan. 16, 2016, *H. Akiyama 24507*, *24517*, and *24525* (all HYO); ibid., Inokawa route, 610 m elev., July 7, 2011, *Y. Ohnishi 120* (HIRO, as *Gammiella tonkinensis*); ibid., Mt. Inokawa-dake, Ikema route, 570 m elev., July 9, 2011, *Y. Ohnishi 431* (HIRO, as *Gammiella tonkinensis*).

Note 1. When Tan (1990) first described *Gammiella touwii* from Mindanao I. (Philippines), he compared it with *G. tonkinensis* and *Aptychella tenuiramea* (Mitt.) P.Tixier. Later Tan & Yu (1999) reduced *G. touwii* to synonym under *G. tonkinensis*, which I do not follow. According to the results of the present molecular phylogeny, *G. touwii* is revealed to be a synonym of *Yakushimabryum subintegra*.

Akiyama (2014) summarized the morphological differences of *Yakushimabryum subintegra* (as *Y. longissimum*) from those of *Y. tonkinense* as follows; (1) smooth, long rectangular, thin walled cells of filamentous gemmae, (2) absence of serration at lower leaf margins, (3) presence of flagelliform, long pendulous branch tips, and (4) habitat preference at higher elevations than *Gammiella tonkinensis*. In Taiwan, northern Vietnam, and Yakushima (South Japan), however, they are rarely found in the same places.

Note 2. Two specimens of *Yakushimabryum subintegrum* collected in central Taiwan have gemmae with rather thick walled and short rectangular cells. In addition, although typical plants of *Y. subintegrum* have leaves with entire basal leaf margins, these two have faint serrations and thus appear similar to *Y. tonkinense*. According to the molecular analyses, however, the Taiwanese plants form a monophyletic clade with the other samples of *Y. subintegrum*. Since only molecular markers of cpDNA were analyzed in the present study, future studies using nuclear DNA sequences will help in resolving this puzzling issue. Our preliminary study based on part of the ITS2 region shows that the two samples from Taiwan form a monophyletic clade with the other samples of *Y. subintegrum*. It should be also noted that there are typical plants of *Y. tonkinensis* in Taiwan as shown below (for example, *H. Akiyama 24296*, HYO).

2-2. **Yakushimabryum tonkinense** (Broth. & Paris) H. Akiyama, **comb. nov.** —Fig. 7a–l.

Basionym: *Clastobryum tonkinense* Broth. & Paris, Revue Bryologique et Lichénologique 35: 47 (1908) ≡ *Aptychella tonkinense* (Broth. & Paris) Broth., Natürlichen Pflanzenfamilien, ed. 2, 11: 406 (1925) ≡ *Gammiella tonkinensis* (Broth. & Paris) B.C. Tan, Bryologist 93: 433 (1990). —Type: Tonkin (North Vietnam), Prov. Vien Yen, S. E. du Tonkin, Tam Dao, 9–1100 m., 1907, *Dr. Eberhardt s.n.* (lecto- in H-BR! stored as *Moire 949*), **lectotype designated here.**

Clastobryum glomerato-propagulifera Toyama, Acta Phytotaxonomica et Geobotanica 4: 214 (1935) ≡ *Clastobryella glomerato-propagulifera* (Toyama) Sakurai, Muscologia Japonica 152 (1954) ≡ *Aptychella glomerato-propagulifera* (Toyama) Seki, Journal of Science of the Hiroshima University, Ser. B, Div. 2, Bot. 12: 72 (1968). —Type: Japan, Kyushu; Mt. Takakuma, Prov. Ohsumi, 8 Aug 1935, *R. Toyama 1111* (holo- in KYO!).

Plants pale green or yellowish green, turning brownish yellow in old specimens, dull or sometime slightly shiny. Primary stems prostrate, tightly attached to substrate, densely branched. Secondary stems usually less than 1 cm long, procumbent or slightly ascending upwards, sparsely branched, more or less teretely foliate; tips never becoming caudate, with a number of gemmae in leaf axils; central strand absent. Rhizoids pale brown, smooth to minutely mammillose. Gemmae clustered, filamentous, uniseriate, 0.4–1.2 mm long, thick walled, pale brown outside, deep green inside, densely to sparsely mammillose. Pseudoparaphyllia absent or short filamentous, 3–5 cells long. Paraphyllia absent. Leaves narrowly to widely spreading even when dry, ovate-lanceolate to ligulate, acute to acuminate, slightly concave, 0.9–1.6 mm long, 0.2–0.4 mm wide, slightly narrowed at base, not decurrent, ecostate; margins more or less curved inwards, distinctly and sharply serrulate to the base. Upper laminal cells narrowly fusiform, ca. 50–70 µm long, ca. 5 µm wide, thin walled, smooth: median laminal cells linear, thin or walls slightly evenly thickened, 80–120 µm long, ca. 5 µm wide, smooth; alar cells arranged in scalariform manner, inner 2–4 rows large rectangular, thin walled, colored, outermost cells more or less inflated, with 1 or 2 rows of short rectangular to quadrate much smaller cells apically. Axillary hairs colorless, uniseriate, 120–150 µm long, with 2 upper long cells and a single, rectangular basal cell. Sexual organs and sporophytes unknown.

Habitat. On branches and stems of shrubs and trees in sun or filtered light, often beside streams, in warm temperate forests; rarely on granite rocks (Yakushima Isl.). *Yakushimabryum tonkinense* is disjunctly distributed throughout its distribution area, sometimes locally abundant especially in northern Taiwan and southwestern Japan. It often forms dense mats on large fallen branches of *Cryptomeria japonica* that have been planted along streams in narrow ravines in warm temperate zones in western Japan especially in locations with high annual rainfall, such as inland in Wakayama, Kochi, Tokushima and Miyazaki Prefectures.

Distribution. China (Yunnan), Japan (Honshu, Shikoku, Kyushu) , Philippines (Luzon), Taiwan, and Vietnam. Nara Prefecture is the northernmost and Kagoshima Pref. (Yakushima) is the southernmost localities of distribution in Japan. Tan (1991) reported this species as *Gammiella tonkinensis* from China (Guangdong Prov.) but did not cite specimens. Li & Pippo (1994) reported it as *Gammiella tonkinensis* from Guangdong Prov., but I have not examined the voucher specimen.

Other specimens examined. **VIETNAM. Lam Dong Co.,** Da Lat, Bidoup-Nui Ba National Park, in the vicinity of Giang Ly Forest Station, Nov. 13, 2014, *H. Akiyama 23985* (HYO, VNM). **Vinh Phuc Co.,** Tam Dao National

Park, in the vicinity of Lodge House (979 m elev.), Nov. 17, 2014, *H. Akiyama 24105* (HYO, VNM); ibid., en route from Lodge House to the city of Tam Dao (1000 m elev.), Nov. 19, 2014, *H. Akiyama 24161* (HYO, VNM); ibid., Tam Dao city, climbing approach to the Television Tower Mountain, 1000–1200 m elev., Nov. 19, 2014, *H. Akiyama 24177b* (HYO, VNM). **PHILIPPINES. Luzon,** Zambales, High Peak (= Mt. Tapulao), Nov. 2004, *V. C. Linis 558-03* (SINU! as *Gammiella tonkinensis*, intermingled with *Aptychella oblongifolia* H. Akiyama). **CHINA. Yunnan Prov.,** Dulong Jiang (River), Longyuan, 1750 m elev., Aug. 27, 1982, *M. Zang 3527* (SINU! as *Clastobryopsis planula*). **TAIWAN. Taoyuan Co.,** Dongyanshan National Forest Recreation Area, 24.83251° N, 121.41051° E, 950 m elev., Oct. 5, 2015, *H. Akiyama 24296* and many others (HYO). **JAPAN. Nara Pref.,** Kawakami-mura, San-no-ko, 500 m elev., Dec. 15, 2013, *M. Kimura 8338* & *8339* (HYO, OSA). **Wakayama Pref.,** Kozagawa-cho, Yugaito valley, Oct. 25, 1962, *Z. Iwatsuki 619d* (NICH); Kumanogawa-cho, Koguchi, Hiradani, ca. 150 m elev., Jan. 10, 1959, *T. Kodama 13964* (NICH, OSA); ibid., 85 m elev., May 16, 2014, *H. Akiyama 23642*, *23643*, *23644*, *23648*, *23649*, *23650* & *23651* (all HYO); Shingu-shi, Kumanogawa-cho, Takimoto, on the way to Horyu-no-taki, 210 m elev., May 16, 2014, *H. Akiyama 23613*, *23615* & *23617* (all HYO); Tanabe-shi, Hongu-cho, Oto-keikoku valley, in the vicinity of Seitani bridge, 113 m elev., May 17, 2014, *H. Akiyama 23662*, *23663* & *23664* (all HYO); Tanabe-shi, Nakahechi-cho, Chikatsuyu, 274 m elev., May 17, 2014, *H. Akiyama 23672* (HYO); Tanabe-shi, Hirase, 197 m elev., May 17, 2014, *H. Akiyama 23673* (HYO); Tanabe-shi, Shimogawashimo, near the entrance of Mizunomi tunnel, 321 m elev., *H. Akiyama 23676* (NICH). **Tokushima Pref.,** Kaiyo-cho, Hirai, Todoraki-no-taki, 260 m elev., March 26, 2017, *H. Akiyama 24932* (HYO). **Kochi Pref.,** Umaji-mura, Yanase, 650 m elev., June 23, 2013, *H. Akiyama 23044* (HYO; DNA voucher); ibid., Mar. 26, 2014, *T. Ohgue 2366* (KYO, HYO); ibid., Mar. 27, 2014, *T. Ohgue 2399* (KYO, HYO); Nakatosa-cho, Onomi, Honokawa, ca. 430 m elev., June 2, 2014, *H. Akiyama 23678*, *23679*, *23680*, *23691*, *23692*, *23699*, *23714* and *23721* (all HYO). **Kumamoto Pref.,** Mizukami-mura, Mt. Ichifusa, 620 m elev., Mar. 19, 2014, *H. Akiyama 23575* (HYO). **Miyazaki Pref.,** Tsuno-cho, at the foot of Mts. Osuzu, Osuzu-keikoku camping site, 500 m elev., May 16, 2013, *H. Akiyama 22896*, *22898*, *22899*, & *22906* (all HYO); ibid., 360–550 m elev., Feb. 21, 1976, *Z. Iwatsuki* & *H. Inoue 1578* & *1780* (both NICH); ibid., Mt. Osuzu, 750 m elev., Nov. 25, 1956, *M. Mizutani 31063* (NICH); Nichinan-shi, Sakatani, Inotani Valley, May 18, 2013, *H. Akiyama 22961*, *22962* & *22963*(all HYO); ibid., Apr. 25–26, 1978, *Z. Iwatsuki 4604a* (NICH); Nichinan-shi, near the Tsubakiyama camping site, upper reach of Kaichigo river, May 17, 2013, *H. Akiyama 22911*, *22924*, *22925*, *22926*, *22936*, *22945* & *22955* (all HYO); Nichinan-shi, Obi, ca. 30 m elev., Feb. 19, 1959, *S. Hattori 21266* (NICH); Nichinan-shi, Kobuze-no-taki, ca. 150 m elev., Apr. 26, 1978, *Z. Iwatsuki 4607* (NICH). **Kagoshima Pref.,** Yakushima, Yakushima-cho, Shirakawa, 190 m elev., Sept. 10, 2016, *N. Hayashida 00609* (HYO); ibid., 215 m elev., Aug. 26, 2016, *N. Hayashida 00582* (HYO); upper stream of Arakawa river, ca. 1230 m elev., *H. Akiyama 24732* (HYO); Osumi Peninsular, Mt. Takakuma , Aug. 8, 1935, *R. Toyama 1111* (KYO; holotype of *Clastobryum glomerato-propaguliferum*).

Note 1. A close interrelationship between *Yakushimabryum tonkinense* and *Y. subintegra* has been suggested from both morphology (Akiyama 2014) and molecular phylogenetic analysis (Akiyama *et al.* 2015) under the names of *Gammiella tonkinensis* and *Y. longissimum*. Present study with more extensive sampling support the same result and it is reflected in the taxonomical treatment of the former species.

Note 2. Specimens from Vietnam deposited at Missouri Botanical Garden (MO) identified as *Gammiella tonkinensis* were found to be *Orientobryum oligonema*; their branches (secondary stems) are complanately foliate, branch leaves long acuminate and with margins minutely serrate or almost entire at the base, and long filamentous gemmae in the upper leaf axils, which can be seen among surrounding leaves. Other previous reports of *G. tonkinensis* from East and Southeast Asia might be based on similar misidentifications.

Note 3. When describing *Clastobryum serrulatum* Cardot & P. de la Varde (type *Andre 103*, PC!) from South India (Maduri, Kodaikanal), Potier de la Varde (1923) compared it with *C. tonkinensis* (≡ *Yakushimabryum tonkinense* in this paper) and suggested their close relationship. It is true that they share lanceolate leaves, scalariform alar cell formation with short rectangular reddish cells and mammillose filamentous gemmae, but the former differs from the latter in its long acuminate leaf apex, prominent serration only on the upper leaf margins, and the long rectangular cells of the filamentous gemmae. Since *C. serrulatum* is known only from the type specimen, which contains only a few plants, the extent of the morphological variation is unknown and thus its taxonomic position remains ambiguous.

Note 4. According to my field observations in southwestern Japan, *Yakushimabryum tonkinense* is often growing at lower elevations than *Y. subintegra*. The former usually grows on tree trunks and branches (rarely on granite rocks or bamboo culms) in *Cryptomeria japonica* plantations at elevations below 1,000 m along narrow ravines with filtered light; *Y. subintegrum* grows on branches and trunks of short trees in elfin forests in more or less windy places at elevations usually higher than 1,000 m. There are, however, some exceptions: I found both *Yakushimabryum tonkinense* and *Y. subintegrum* growing in the same places in northern Vietnam (Tam Dao N. P.) and in southwestern Japan (central part of Yakushima). Even *Orientobryum oligonema* coexists with these two species at Tam Dao N. P. in northern Vietnam.

Note 5. As pointed by Akiyama *et al.* (2017), *Aptychella tamdaoensis* P.Tixier described by Tixier (1966) from northern Vietnam (Tam Dao N. P., Sept. 6, 1925, *V. Demange s.n.*) might be conspecific with *Yakushimabryum tonkinense.* Unfortunately, I was not able to locate the type specimen.

Note 6. Plants collected from Luzon Isl. in the Philippines (*Linis 558-03*, SINU) have slender filamentous stems and appear similar to *Gammiella touwii* (as *Yakushimabryum subintegrum* in this study). Unfortunately it lacks gemmae. I identified it as *Y. tonkinense* because the stems are not fragile as in *Y. subintegrum* and the basal leaf margins are distinctly serrulate.

2-3. Yakushimabryum brevigemmium
H. Akiyama, **sp. nov.**—Fig. 6.

Closely related to *Yakushimabryum subintegrum*, but differing in the 5 or 6 celled, short fusiform gemmae clustered in the leaf axils on the upper portion of the branches.

Typus. VIETNAM, Vinh Phuc Co., Tam Dao National Park, en route from the Lodge House (979 m elev.) to the summit of Mt. Tam Dao 1 (1365 m), 21°28' N, 105°38' E, 1355 m., Nov. 18, 2014, *H. Akiyama 24142* (holo- in HYO, iso- in BM, L, NY, PHH, VNM).

Plants dark green, not shiny. Primary stems short, densely branched, tightly attached to substrate by dense rhizoids. Secondary stems to 1.5 cm long, pinnately branched, teretely foliate; tips more or less caudate, with a number of gemmae in leaf axils; central strand absent. Branches to 7 mm long. Rhizoids pale brown, sparsely papillose. Gemmae directly formed from epidermal cells of secondary stems, clustered, short fusiform, thin walled, pale brown outside, blackish green, with 5 or 6 cells, 110–125 μm long, smooth. Paraphyllia absent. Pseudoparaphyllia absent. Stem and branch leaves similar in size and shape, patent when dry, spreading when moist, lanceolate, acuminate to acute, 2–2.2 mm long, 0.4–0.5 mm wide, narrowed at base, not decurrent, ecostate; margins minutely serrulate apically, basally entire. Upper laminal cells fusiform, ca. 50 μm long, thin walled, smooth: median laminal cells linear, thin walled, 80–100 μm long, 5 μm wide, smooth, becoming shorter toward margin; alar cells arranged in scalariform manner, moderately thick walled, with large rectangular cells in basal 2 or 3 rows, outermost cells thin walled and more or less inflated, with 1 or 2 rows of short rectangular to quadrate cells above. Axillary hairs pale brown, uniseriate, to 250 μm long, with 3 or 4 upper linear cells and a single, long rectangular basal cell. Sexual organs and sporophytes unknown.

Habitat. Forming compact pendulous colonies on slender branches of short shrubs in a rather windy place with filtered light on a mountain ridge covered with short shrubs (Fig. 6 a–c).

Distribution. Northern Vietnam.

Other specimens examined. Only a single specimen (type) is so far known.

Note 1. The aggregated, short fusiform, blackish-green, well-septate gemmae in the leaf axils are the most distinguishing feature of *Yakushimabryum brevigemmium*. It appears similar in external morphology to *Yakushimabryum subintegrum* and grows in a similar habitat. According to the present phylogenetic analyses, it is sister to the clade including both *Y. subintegrum* and *Y. tonkinense* (Figs. 1 & 2)

3. **Pseudotrismegistia** H. Akiyama & H. Tsubota in Acta Phytotaxonomica et Geobotanica 52: 85 (2002) (Sematophyllaceae *s. lat.*)

Type species: *Pseudotrismegistia undulata* (Broth. & Yasuda) H. Akiyama & H. Tsubota.

In describing *Pseudotrismegistia*, Akiyama & Tsubota (2001) pointed out that the type species of the genus, *P. undulata* (Broth. & Yasuda) H. Akiyama & H. Tsubota, has a close affinity to *Mastopoma subfiliferum* Horik. & Ando, which is endemic to Doi Inthanon, northern Thailand. These two species grow side by side at higher elevations of the mountain (2,300–2,500 m in elev.) and they are both large, pinnately branching plants, with more or less ligulate leaves distally, well differentiated alars with thick walled rectangular cells, ovoid capsules on setae 3.5 to 6 cm long, and a complete hypnoid peristome. Their close relationship was also supported in the present phylogenetic analysis. Yu *et al.* (2007) provided detailed notes on *Heterophyllium amblystegum* (Mitt.) J. Yu, S. He & Crosby from the Himalaya. From a comparison of the type specimen and from their detailed illustration, *M. subfiliferum* is revealed to be a synonym of *H. amblystegum* and thus the following taxonomic treatment is provided.

Key to the species

1a. Leaves 2–3 mm long, falcate, narrowly ligulate upper portion plane .... 3.1. *P. amblystega*

1b. Leaves to 5 mm long, not falcate, ligulate upper portion distinctly undulate .... *P. undulata* (see Akiyama & Tsubota 2001)

3-1. **Pseudotrismegistia amblystega** (Mitt.) H. Akiyama, **comb. nov.**

Basionym: *Stereodon amblystegus* Mitt., Journal of the Proceedings of the Linnean Society, Botany Supplement 2: 97 (1859) ≡ *Hypnum amblystegum* (Mitt.) A. Jaeger, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1877–1888: 301(1880) ≡ *Brotherella amblystega* (Mitt.) Broth., Natürlichen Pflanzenfamilien, ed. 2, 11: 425 (1925) ≡ *Calohypnum amblystegum* (Mitt.) Sakurai, Japanese Journal of Botany 25: 220 (1950) ≡ *Pylaisiadelpha amblystega* (Mitt.) W.R.Buck, Yushania 1(2): 11 (1984) ≡ *Heterophyllium amblystegum* (Mitt.) J. Yu, S. He & Crosby, Novon 17: 332 (2007). —Type: Sikkim, *J. D. Hooker 973* (lecto- in NY!, isolecto- in BM).

Mastopoma subfiliferum Horik. & Ando, Nature and Life in Southeast Asia 3: 36 (1964). —Type: Thailand, Doi Inthanon, on trunk, mossy forest, 2300–2550 m, Jan. 9, 1958, *K. Yoda 67764* (holo- in HIRO!), **syn. nov.** Detailed descriptions and a good illustration were provided by Horikawa & Ando (1964) as *Mastopoma subfiliferum* and by Yu *et al.* (2007) as *Heterophyllium amblystegum*.

Habitat. According to observation in Doi Inthanon, northern Thailand, *Pseudotrismegistia amblystega* occupies a habitat similar to that of *P. undulata* on the base of tree trunks in upper montane evergreen forests; sometimes they grow side-by-side.

Distribution. Northern India (Sikkim) and northern Thailand (Doi Inthanon).

Other specimens examined. **THAILAND.** Ching Mai Co., Doi Inthanon, around the summit area, 2550 m elev., Dec. 5, 2000, *Akiyama Th-2, 69* and *116* (all HYO): ibid., Ang Ka Trail, 2500 m elev., March 9, 2011, *Akiyama & Printarakul 1479* (with sporophytes; HYO); ibid., 2300 m elev., Jan. 10, 2010, *H. Akiyama et al. 1021*, *1026* (male) & *1073* (all HYO).

Note 1. Distinguishing features of this species can be summarized as follows: (1) Plants prostrate, densely pinnately branched; (2) stem and branch leaves narrowly ligulate above, strongly falcate; (3) rectangular alar cells somewhat colored and arranged in a scalariform manner; (4) costa absent; (5) setae 4–5 cm long; and (6) capsules short ovoid with double hypnoid peristome.

Note 2. In appearance, such as in the branching pattern of the stems, strongly curled leaves, and long setae (to 5 cm long) with short ovoid capsules, *Pseudotrismegistia amblystega* appears similar to *Heterophyllium*, but the present molecular analysis (based on a sample from northern Thailand previously reported as *Mastopoma subfiliferum*) suggests a closer relationship to *P. undulata*, not to *H. affine* (Hook.) M. Fleisch.

Keys to *Orientobryum, Yakushimabryum* and related genera and species in the Pylaisiadelphaceae *s. str.*
(*Clastobryum* and members of subfamily Heterophyllioideae, i.e., *Heterophyllium*, *Mastopoma*, *Pseudotrismegistia*, and *Trismegistia* are not treated)

1a. Laminal cells more or less papillose 2
1b. Laminal cells smooth 3
2a. Plants filamentous, forming thin carpets on tree trunks; leaves less than 0.5 mm long, deeply concave and apiculate; laminal cells rhomboid; alars scarcely differentiated .... *Fauriella*
2b. Plants various; leaves usually more than 1 mm long, plane or slightly concave, acute to acuminate; laminal cells linear; alars more or less differentiated .... *Taxithelium*
3a. Plants usually filamentous, creeping on substrate; dormant branch buds covered with filamentous pseudoparaphyllia; alar slightly differentiated with several quadrate thin walled cells .... *Isopterygium*
3b. Plants various, not filamentous; dormant branch buds various (usually naked or surrounded by triangular or leafy pseudoparaphyllia); alars more or less clearly differentiated, with large thin walled cells or a number of quadrate to rectangular, thick walled cells (except in *Pylaisiadelpha*) 4
4a. Caducous flagelliform branchlets almost always present .... *Isocladiella*
4b. Caducous flagelliform branchlets absent (except for short caducous branchlets in *Orientobryum*) 5
5a. Gemmiferous branches differentiated, caudate at tips; gemmae filamentous, smooth .... *Aptychella*
5b. Gemmiferous branches not differentiated from ordinary branches; gemmae, if present, filamentous or short fusiform, smooth or mammillose 6
6a. Gemmae, if present, smooth, filamentous or short rhomboid (except in *Yakushimabryum tonkinense*); alar cells various in size and shape; basal row with larger and more or less inflated cells .... *Yakushimabryum*
6b. Gemmae, if present, filamentous and mammillose; alar cells quadrate to short rectangular; cells of basal row not highly differentiated 7
7a. Stem and branch leaves less than 0.8 mm long .... *Gammiella ceylonensis*
7b. Stem and branch leaves more than 1 mm long 8
8a. Leaves deeply concave 9
8b. Leaves plane or slightly concave 10
9a. Plants more or less shiny; leaves ovate to ovate-lanceolate, abruptly narrowed into acute to shortly acuminate apex .... *Gammiella pterogonoides*
9.b Plants dull; leaves lanceolate to oblong lanceolate, gradually narrowed into acute apex (after Tan & Yu 1999) .... *Gammiella panchienii*
10a. Alar cells with basal single row with larger and thin walled cells; capsules more or less curved .... *Wijkia + Brotherella+ Pylaisiadelpha*
10b. Alar cells quadrate to rectangular, arranged in scalariform manner; capsules straight. .... *Yakushimabryum*

I thank Ms. Thien Tam Luong (University of Sciences, Vietnam), Mr. Dinh Nhat Lam (Southern Institute of Ecology, Vietnam), Dr. Monica Suleiman (Universiti Malaysia Sabah, Malaysia), Dr. Kanya Santanachote and Dr. Narin Printarakul (Chiang Mai University, Thailand), Dr. Yong Kien Thai (University of Malaya, Malaysia), Dr. S. Lin (Tsunhai University, Taiwan), Mr. H. Ohara (YNAC, Japan), Mr. N. Hayashida (Yakushima, Japan), Mr. T. Mizuma (Amamioshima, Japan), for their kind help in the field surveys, Dr. Hidetoshi Nagamasu (Kyoto University Museum) for his valuable suggestions on the nomenclature of *Clastobryum tonkinensis*. I am in debt to the curators of BM, FH, H, HIRO, HYO, KYO, L, NICH, NY, OSA, PC, SING, SINU, and TNS for loans of specimens. I also thank to Dr. W. R. Buck (New York Botanical Garden) for linguistic corrections of the text. I owe very much to the Office of the National Research Council of Thailand (NRCT) for permission to conduct field research in Doi Inthanon National Park, the authorities concerned in Japan for allowing for collections within National Parks on Yakushima, Hachijyoshima, Amamioshima, and Tokunoshima. I would like to thank two anonymous referees for their valuable comments on the manuscript. This study was financially supported by JSPS KAKENHI no. 24570108 and no. 16K07488 to the author, and no. 24255007 to Dr. M. Kanzaki (Kyoto University).

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Received December 14, 2016; accepted April 26, 2017

APPENDIX. Eighty three samples used in analyses and their accession numbers (in order of *rps4*, *trnL–F*, and *rbcL*). Samples with new accessions are indicated with an asterisk (*) before species name and with detailed voucher information in curly brackets. Scientific names used in Figs. 1 and 2 are shown in parentheses.

Acroporium pungens AY908207 AF161121 AF233572 [*W. R. Buck 33028* (NY)]

Acroporium secundum GQ254028 GQ254047 GQ254037 [Y. Liu & M. Z. Wang 3979 (PC)]

*Aptychella brevinervis*1 AB938185 LC059910 LC059955 [*H. Akiyama 22752* (HYO)]

*Aptychella brevinervis*2 LC059870 LC059915 LC059958 [*H. Akiyama23897* (HYO)]

Aptychella oblongifolia LC059873 LC059920 LC059962 [*H. Akiyama & N. Printarakul 1473* (HYO)]

Aptychella proligera LC059857 LC059926 LC059966 [*Schäfer-Verwimp & Verwimp 26645* (HYO)]

Aptychella pseudobrevinervis LC059876 LC059936 LC059973 [*Akiyama & Printarakul 1172* (HYO)]

*Aptychella robusta*1 LC059883 LC059938 LC059981 [*H. Akiyama 23724* (HYO)]

*Aptychella robusta*2 AB971901 LC059943 LC059980 [*H. Akiyama 23272* (HYO)]

**Brothrella henonii* LC229584 LC229579 LC229574 [Japan, Mie, Ise, Amano-iwato, *H. Akiyama 24331* (HYO)]

Brotherella recurvans AY908227 — L13475 [*W.R. Buck 31506* (NY)]

**Chionostomum rostratum* LC229585 LC229580 LC229575 [Vietnam, Tam Dao, *H. Akiyama 24136* (HYO)]

**Clastobryum glabrescens* LC195386 LC195445 LC195303 [Taiwan, Taichung, Mt. Dasyueshan, *H. Akiyama 23264* (HYO)]

**Clastobryum scalare* LC195387 LC195446 LC195304 [Malaysia, Sabah, Gunung Alab, *H. Akiyama 23537* (HYO)]

**Clastobryum scalare* LC195388 LC195447 LC195305 [Malaysia, Pahang, Genting Highland, *H. Akiyama 23866* (HYO)]

**Clastobryum spiculiferum* LC195389 LC195448 LC195306 [Malaysia, Cameron Highland, *H. Akiyama 23907* (HYO)]

**Climacium dendroides* LC195390 LC195449 LC195307 [Japan, Nagano Pref., Yatsugatake, *H. Akiyama 24283* (HYO)]

**Fauriella tenuis* LC229586 LC229581 LC229576 [Japan, Kagoshima, Tokunoshima, *H. Akiyama 24602* (HYO)]

**Gammiella ceylonensis* LC195392 LC195451 LC195309 [Vietnam, Tam Dao, *H. Akiyama 24126* (HYO)]

**Gammiella ceylonensis* LC195391 LC195450 LC195308 [Japan, Kagoshima Pref., Yakushima, *H. Akiyama 22754* (HYO)]

Gammiella panchienii LC059886 LC059946 LC059985 [*J. Shevock 32051* (CAS)]

**Gammiella pterogonioides* AB971903 LC059947 LC059986 [Thailand, Doi Inthanon, *H. Akiyama & N. Printarakul 1554* (HYO)]

**Gammiella pterogonioides* LC195393 LC195452 LC195310 [Thailand, Doi Inthanon, *H. Akiyama & N. Printarakul 1244* (HYO)]

**Heterophyllium affine* LC195414 LC195473 LC195330 [Japan, Nagano Pref., Mt. Yatsugatake, *H. Akiyama 24288* (HYO)]

**Heterophyllium amblystegum* (as *Mastopoma subfiliferum*) LC215375 LC215381 LC215378 [Thailand, Doi Inthanon, *H. Akiyama* & *N. Printarakul 1479* (HYO)]

Isocladiella surcularis LC059890 LC059950 LC059989 [*H. Akiyama 23476* (HYO)]

**Isocladiella surcularis* LC195415 LC195474 LC195331 [Japan, Wakayama Pref., Shingu-shi, *H. Akiyama 23658* (HYO)]

Isopterygium propaguliferum LC059889 LC059951 LC059990 [*H. Akiyama 26066* (HYO)]

Isopterygium tenerum AF143037 AF161130 AF233569 [clone ID IT89]

**Mastopoma uncinifolium* LC195416 LC195475 LC195332 [Malaysia, Sabah, Kinabalu Park, *H. Akiyama 23427* (HYO)]

**Orientobryum oligonema*1 (*Clastobryum oligonema*) LC195420 LC195479 LC195336 [Vietnam, Bidoup-Nui Ba, *H. Akiyama 24086* (HYO)]

**Orientobryum oligonema*2 (*Clastobryum oligonema*) LC195417 LC195476 LC195333 [Thailand, Doi Inthanon, *H. Akiyama et al. 252* (HYO)]

**Orientobryum oligonema*3 (*Clastobryum oligonema*) LC195418 LC195477 LC195334 [Thailand, Doi Inthanon, *H. Akiyama & N. Printarakul 1431* (HYO)]

**Orientobryum oligonema*4 (*Clastobryum oligonema*) LC195422 LC195481 LC195338 [Vietnam, Ba *Na-Nui Chua, S. He & Khuang 42616* (MO)]

**Orientobryum oligonema*5 (*Clastobryum oligonema*) LC195423 LC195482 LC195339 [Vietnam, Ba *Na-Nui Chua, S. He & Khuang 42623* (MO)]

**Orientobryum oligonema*6 (*Clastobryum oligonema*) LC195421 LC195480 LC195337 [Vietnam, Tam Dao, *H. Akiyama 24183* (HYO)]

**Orientobryum ovalifolium* (*Clastobryum oligonema*) LC195419 LC195478 LC195335 [Vietnam, Bidoup-Nui Ba, *H. Akiyama 24006* (HYO)]

**Papillidiopsis complanata* LC229587 LC229582 LC229577 [Japan, Kagoshima, Amamioshima, *H. Akiyama 24375* (HYO)]

**Pleuroziopsis ruthenica* LC195424 LC195483 LC195340 [Japan, Nagano Pref., Yatsugatake, *H. Akiyama 24260* (HYO)]

**Pseudotrismegistia undulata* LC195425 — LC195484 [Thailand, Doi Inthanon, *H. Akiyama & N. Printara-*

kul 1339 (HYO)]

Pylaisiadelpha tenuirostris AF143053 AF161146 AB051219 [clone ID PT56]

**Pylaisiadelpha tristo-viride* LC059888 LC059949 LC059988 [Japan, Kochi Pref., Umaji-mura, *N. Nishimura 13147* (HYO)]

**Sematophyllum subhumile* LC195427 LC195486 LC195341 [Thailand, Doi Inthanon, *H. Akiyama & N. Printarakul 1423* (HYO)]

**Sematophyllum subpinnatum* LC229588 LC229583 LC229578 [Japan, Kagoshima, Mt. Obi, *H. Akiyama 23749* (HYO)]

Taxithelium planum AY908231 AF161147 — [*A. Newton et al. 4641* (per. herb.)]

Trichosteleum papillosum AF143056 AF161149 AF233574 [clone ID TP36]

**Trismegistia panduriformis* var. *prionodontella* LC195428 LC195487 LC195342 [Malaysia, Sabah, Kinabalu Park, *H. Akiyama 23460* (HYO)]

**Wijkia deflexifolia* LC215377 LC215383 LC215380 [Japan, Kagoshima Pref., Yaku-cho, Yakushima, *H. Akiyama22730* (HYO)]

**Wijkia hornschuchii* LC215376 LC215382 LC215379 [Japan, Kagoshima Pref., Yaku-cho, Yakushima, *H. Akiyama 24775* (HYO)]

**Yakushimabryum brevigemmium* LC195429 LC195488 LC195343 LC195376 [Vietnam, Vinh Phuc Co., Tam Dao NP, *H. Akiyama 24142* (holotype, HYO)]

*Yakushimabryum subintegrum*1 (*Y. longissimum*) LC059891 LC059952 LC059991 [Japan, Kagoshima Pref., Yaku-cho, Yakushima, *H. Akiyama 22765* (HYO)]

*Y*akushimabryum subintegrum*2 (*Y. longissimum*) LC195431 LC195490 LC195344 [Japan, Tokyo Pref., Hachijyojima, Nishiyama, *H. Akiyama 22802* (HYO)]

**Yakushimabryum subintegrum*3 (*Y. longissimum*) LC195432 LC195491 LC195345 [Japan, Tokyo Pref., Hachijyojima, Miharayama, *H. Akiyama 22834* (HYO)]

**Yakushimabryum subintegrum*4 (*Y. longissimum*) LC195435 LC195494 LC195348 [Japan, Kagoshima Pref., Kanoya-shi, Mt. Obi, *H. Akiyama 23344* (HYO)]

**Yakushimabryum subintegrum*5 (*Y. longissimum*) LC195436 LC195495 LC195349 [Japan, Kagoshima Pref., Kanoya-shi, Mt. Obi, *H. Akiyama 23357* (HYO)]

**Yakushimabryum subintegrum*6 (*Y. longissimum*) LC195437 LC195496 LC195350 [Japan, Kagoshima Pref., Kanoya-shi, Mt. Inabi, *H. Akiyama 23771* (HYO)]

**Yakushimabryum subintegrum*7 (*Y. longissimum*) LC195433 LC195492 LC195346 [Taiwan, Taichung, Hshuepa National Park, Syuejin Recreation Area, *H. Akiyama 23153-b* (HYO)]

**Yakushimabryum subintegrum*8 (*Y. longissimum*) LC195434 LC195493 LC195347 [Taiwan, Taichung, Daisetsu, *H. Akiyama 23284* (HYO)]

**Yakushimabryum subintegrum*9 (*Gammiella touwii*) LC195439 LC195498 LC195352 [Malaysia, Pahang, Cameron Highland, *H. Akiyama 23913* (HYO)]

**Yakushimabryum subintegrum*10 (*Gammiella touwii*) LC195438 LC195497 LC195351 [Malaysia, Pahang, Cameron Highland, *H. Akiyama 23878* (HYO)]

**Yakushimabryum subintegrum*11 (*Aptychella subintegra*) LC195441 LC195500 LC195353 [Vietnam, Vinh Phuc Co., Tam Dao NP, *H. Akiyama 24119* (HYO)]

**Yakushimabryum subintegrum*12 (*Aptychella subintegra*) LC195442 LC195501 LC195354 [Vietnam, Vinh Phuc Co., Tam Dao NP, *H. Akiyama 24127* (HYO)]

**Yakushimabryum subintegrum*13 (*Y. longissimum*) LC195443 LC195502 LC195355 [Japan, Kagoshima Pref., Amamioshima, *H. Akiyama 24471* (HYO)]

**Yakushimabryum subintegrum*14 (*Y. longissimum*) LC195444 LC195503 LC195356 [Japan, Kagoshima Pref., Tokunoshima, *H. Akiyama 24517* (HYO)]

**Yakushimabryum tonkinense*1 (*Gammiella tonkinensis*) LC195411 LC195472 LC195329 [Japan, Kagoshima Pref., Yaku-cho, Yakushima, Arakawa, *N. Hayashida 00582* (HYO)]

**Yakushimabryum tonkinense*2 (*Gammiella tonkinensis*) LC195410 LC195469 LC195326 [Japan, Kagoshima Pref., Yaku-cho, Yakushima, Arakawa, KKW, *H. Akiyama 24732* (HYO)]

**Yakushimabryum tonkinense*3 (*Gammiella tonkinensis*) LC195396 LC195455 LC195313 [Japan, Miyazaki Pref., Nichinan-shi, Tsubakiyama, *H. Akiyama 22924* (HYO)]

**Yakushimabryum tonkinense*4 (*Gammiella tonkinensis*) LC195394 LC195453 LC195311 [Japan, Miyazaki Pref., Tsuno-cho, Osuzu, *H. Akiyama 22899* (HYO)]

**Yakushimabryum tonkinense*5 (*Gammiella tonkinensis*) LC195397 LC195456 LC195314 [Japan, Miyazaki Pref., Nichinan-shi, Inotani, *H. Akiyama 22961* (HYO)]

**Yakushimabryum tonkinense*6 (*Gammiella tonkinensis*) LC195398 LC195457 LC195315 [Japan, Kochi Pref., Umaji-mura, Ganmaki-dani, *H. Akiyama 23044* (HYO)]

**Yakushimabryum tonkinense*7 (*Gammiella tonkinensis*) LC195413 LC195471 LC195328 [Japan, Kochi Pref., Umaji-mura, Nakagawa, *T. Ohgue 2399* (KYO)]

**Yakushimabryum tonkinense*8 (*Gammiella tonkinensis*) LC195406 LC195465 LC195323 [Japan, Kochi Pref., Nakatosa-cho, Honokawa, *H. Akiyama 23679* (HYO)]

**Yakushimabryum tonkinense*9 (*Gammiella tonkinensis*) LC195407 LC195466 LC195324 [Japan, Kochi Pref., Nakatosa-cho, Honokawa, *H. Akiyama 23680* (HYO)]

**Yakushimabryum tonkinense*10 (*Gammiella tonkinensis*)

LC195412 LC195470 LC195327 [Japan, Nara Pref., Kawakami-cho, *M. Kimura 8339* (HYO)]

***Yakushimabryum tonkinense*11 (*Gammiella tonkinensis*) LC195399 LC195458 LC195316 [Japan, Kumamoto Pref., Mt. Ichifusa, *H. Akiyama 23575* (HYO)]

**Yakushimabryum tonkinense*12 (*Gammiella tonkinensis*) LC195400 LC195459 LC195317 [Japan, Wakayama Pref., Shingu-shi, Takimoto, *H. Akiyama 23615* (HYO)]

**Yakushimabryum tonkinense*13 (*Gammiella tonkinensis*) LC195401 LC195460 LC195318 [Japan, Wakayama Pref., Shingu-shi, Koguchi, *H. Akiyama 23648* (HYO)]

**Yakushimabryum tonkinense*14 (*Gammiella tonkinensis*) LC195402 LC195461 LC195319 [Japan, Wakayama Pref., Shingu-shi, Ohto, *H. Akiyama 23662* (HYO)]

**Yakushimabryum tonkinense*15 (*Gammiella tonkinensis*) LC195403 LC195462 LC195320 [Japan, Wakayama Pref., Tanabe-shi, Kinro, *H. Akiyama 23672* (HYO)]

**Yakushimabryum tonkinense*16 (*Gammiella tonkinensis*) LC195404 LC195463 LC195321 [Japan, Wakayama Pref., Tanabe-shi, Hirase, *H. Akiyama 23673* (HYO)]

**Yakushimabryum tonkinense*17 (*Gammiella tonkinensis*) LC195405 LC195464 LC195322 [Japan, Wakayama Pref., Tanabe-shi, Shimokawashita, *H. Akiyama 23676* (HYO)]

*Yakushimabryum tonkinense*18 (*Gammiella tonkinensis*) LC059887 LC059948 LC059987 [Vietnam, Bidoup-Nui, Ba *H. Akiyama 23985* (HYO)]

**Yakushimabryum tonkinense*19 (*Gammiella tonkinensis*) LC195409 LC195468 LC195325 [Taiwan, Taipei, Tongwenshan, *H. Akiyama 24296* (HYO)]